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A Quarter Century of Monitoring the Fish Assemblages of San Diego Bay, California from 1995 to 2019

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Abstract.—A time series of 22 samples collected in April and July were taken of the fish assemblages of San Diego Bay over 11 non-consecutive years from 1995 to 2019. Each sample consisted of four ecoregions using a variety of collection methods designed to assess all components of the ichthyofauna. These samples yielded a total of 525,288 fishes belonging to 90 species and weighing 3,507 kg over the 25-year period. Northern anchovy was the most abundant fish species comprising 41% of the total catch despite its virtual absence near the end of the survey period, followed by topsmelt, slough anchovy, shiner perch, and Pacific sardine. Round stingrays dominated in weight constituting more than 27% of the total biomass taken followed by spotted sand bass, and northern anchovy. Approximately 64% of all individual fish captured in San Diego Bay during this study were juveniles. In a canonical correlation analysis, temperature, distance from the mouth of the bay, and salinity accounted for nearly 93% of the variance in individual species abundances. In the time series analyses, we found all three potential temporal patterns of fish species abundance, biomass, and diversity, namely: 1) significant decreases over time, 2) significant increases over time, and 3) no significant change over time. Abundance of eight of the top 35 species (including northern anchovy, topsmelt, slough anchovy, and shiner perch) and all forage species combined decreased over the study. Two species increased significantly in abundance, spotted sand bass and dwarf perch. Whereas, total abundance, total biomass, species richness, Shannon diversity, and the majority (71%) of species abundances did not change over the 25-year period. Despite various environmental perturbations and the general trends of decreases in larval and fish abundance indices over the Southern California Bight in recent years, the stability in species richness and composition over time reflects the generally resilient nature of the fish assemblage structure of San Diego Bay that has been maintained by active management including restoration practices.

Bays and estuaries normally are considered important nursery areas for coastal marine fishes (Cronin and Mansueti 1971; Haedrich and Hall 1976). The warm spring-summer water temperatures coupled with high productivity enable these environments to support

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large numbers of juvenile fish (Allen 1982). Southern California bays and estuaries are relatively small and scarce when compared to the large, river-dominated estuaries common in many other parts of the world (Horn and Allen 1981). They do, however, function as nursery areas in the classical sense for some species. At least one commercially important species (California halibut, *Paralichthys californicus*) relies heavily on southern California bays and estuaries as nursery areas (Allen 1988). Juveniles of non-commercial fishes are extremely abundant and usually dominate the fish assemblages of bays and estuaries in the Southern California Bight (SCB; Allen 1982). Many of these abundant, non-commercial species (e.g., gobies, anchovies, and silversides) are important forage fishes for commercial fish species (Horn 1980) and sea birds. An often-overlooked characteristic of the fish assemblages from southern California bays and estuaries is that these habitats support a unique set of species found nowhere else in the SCB (Horn 1980; Horn and Allen 1981; Allen 1985). Considering juvenile fish recruitment and the limited amount of habitat bays and estuaries represent in the SCB, long-term tracking of this assemblage is necessary for resource management at a variety of scales.

San Diego Bay is the largest naturally occurring marine embayment between San Francisco and Scammon's Lagoon in central Baja California containing approximately 4,858 ha of marine habitat[1]. With four distinct hydrodynamic regions, the bay is delineated by latitudinal variation in temperature and salinity (Largier et al. 1996, 1997). The north and north-central ecoregions are dominated by tidal exchange with the ocean whereas the waters in the adjacent south-central and south ecoregions are driven by a delicate density balance between changes in temperature and salinity throughout the year. Only the south ecoregion appears comparable to other southern California bays and estuaries in terms of physical and biotic characteristics. The bay provides expansive and diverse habitats for fishes including deep channels, marinas, and extensive shallows largely covered with eelgrass (*Zostera marina*) (Obaza et al. 2015).

In general, SCB fish species found in various sub-habitats of bays and estuaries represent different niches. California killifish (*Fundulus parvipinnis*) and longjaw mudsuckers (*Gillichthys mirabilis*) are most abundant in the shallow tidal channels of marsh habitats. Topsmelt (*Atherinops affinis*), striped mullet (*Mugil cephalus*), deepbody anchovy (*Anchoa compressa*), and slough anchovy (*A. delicatissima*) inhabit the water column of both main channels and near shorelines, although topsmelt and striped mullet feed on the bottom. Arrow goby (*Clevelandia ios*), shadow goby (*Quietula y-cauda*), cheekspot goby (*Ilypnus gilberti*) and yellowfin goby (*Acanthogobius flavimanus* - introduced) as a group of gobies (Perciformes: Gobiidae) are the most abundant benthic fishes along the shorelines. Deeper channels are inhabited mainly by residents and seasonal migrants including black perch (*Embiotoca jacksoni*), diamond turbot (*Pleuronichthys guttulatus*), juvenile California halibut, spotted sand bass (*Paralabrax maculatofasciatus*), juvenile barred sand bass (*Paralabrax nebulifer*), yellowfin croaker (*Umbrina roncador*), and round stingray (*Urobatis halleri*) (Horn and Allen 1981).

Understanding the utilization of sub-habitats by fishes and the drivers that influence distribution and abundance of fishes is an important aspect of natural resource management. Distribution and abundance of fishes throughout habitats in California nearshore waters,

[1] U.S. Department of Defense and Port of San Diego. 2013. San Diego Bay Integrated Natural Resources Management Plan. Naval Facilities Engineering Command Southwest and Port of San Diego, San Diego, CA. September 2013.

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bays, and estuaries are influenced by several biotic and abiotic factors (Hubbs 1948; Horn and Allen 1981; Pondella et al. 2005; Winder and Jassby 2011; Pondella et al. 2019). Additionally, in the SCB both large-scale cyclical climatic events (e.g., El Niño/Southern Oscillation) and processes occurring at the local level can greatly influence fishes at a variety of scales (Barber and Chavez 1983; Williams et al. 2007; Koslow et al. 2015).

San Diego Bay is host to approximately half of the eelgrass in southern California, the vast majority of which is in the south ecoregion[2]. Eelgrass is a foundational species that acts as a nursery ground for many nearshore fishes (Allen et al. 2002) and may provide refuge from long-term disturbances (Obaza et al. 2015). Eelgrass declined in the bay through the early to middle part of the 20th century due to poor water and sediment quality (Peeling 1974) but has rebounded over the last half-century through regulations, remediation (Fairey et al. 1998), and restoration efforts (*e.g.*, Pondella et al. 2006) by the United States Navy and Port of San Diego. Due to these active restoration efforts and improvements in water quality, aerial coverage of eelgrass increased in the bay from a low of 441.7 ha in 1993 to the highest reported coverage in 2020 of 1051.3 ha.[3] Conversely, 90% of eelgrass disappeared from Morro Bay in central California over the last 15 years (Walter et al. 2018), and fish composition subsequently changed from an eelgrass habitat specialist dominated community to a soft-bottom generalist dominated community (O'Leary et al. 2021).

Allen et al. (2002) completed the only comprehensive study of the fish populations of the entire San Diego Bay with quarterly sampling from July 1994 to July of 1999. In this study, the species composition, relative abundances, and biomass contributions of the bay fishes remained very similar since the 1960s[4]. Topsmelt, northern anchovy, slough anchovy, arrow goby, barred pipefish (*Syngnathus auliscus*), and California killifish were the most numerically abundant species found in San Diego Bay while round stingrays, California halibut, and spotted sand bass dominated in terms of biomass. They also concluded that sampling in the months of April and July yielded the highest abundance and diversity of fishes and recommended to funding sponsors (U.S. Navy and Port of San Diego) that future long-term sampling in those months best represent the status of fish populations in San Diego Bay.

From 1994 to 2019, there have been notable environmental perturbations, including variation in the Pacific Decadal Oscillation (PDO), Oceanographic Nino Index (ONI), North Pacific Gyre Oscillation (NPGO), Multivariate ENSO Index (MEI), an increase in Sea Surface Temperature (SST) and a marine heatwave (Bond et al. 2015; Jacox et al. 2016; Gentemann et al. 2017; Zhang et al. 2019). During this time frame, there have been noted declines of nearshore fishes and larval fishes in this assemblage (Miller and McGowan 2013; Koslow et al. 2015). This study's length allowed a unique opportunity to examine these macroscale long-term trends and disturbances against the backdrop of active management, including multiple restoration activities, to assess whether this system is

[2] Bernstein, B., K. Merkel, B. Chesney, and M. Sutula. 2011. Recommendations for a Southern California Regional Eelgrass Monitoring Program. Southern California Coastal Water Research Project. Tech. Rept. 632.

[3] Merkel & Associates. 2020. 2020 San Diego Bay Eelgrass Inventory. Prepared for Naval Facilities Engineering Systems Command Southwest, San Diego, CA. December 2020.

[4] Ford, R.F. 1968. Marine organisms of South San Diego Bay and the ecological effects of power station cooling water. A pilot study conducted for San Diego Gas and Electric Co., California, Environmental Engineering Laboratory Tech. Rept. On Contract C-188.

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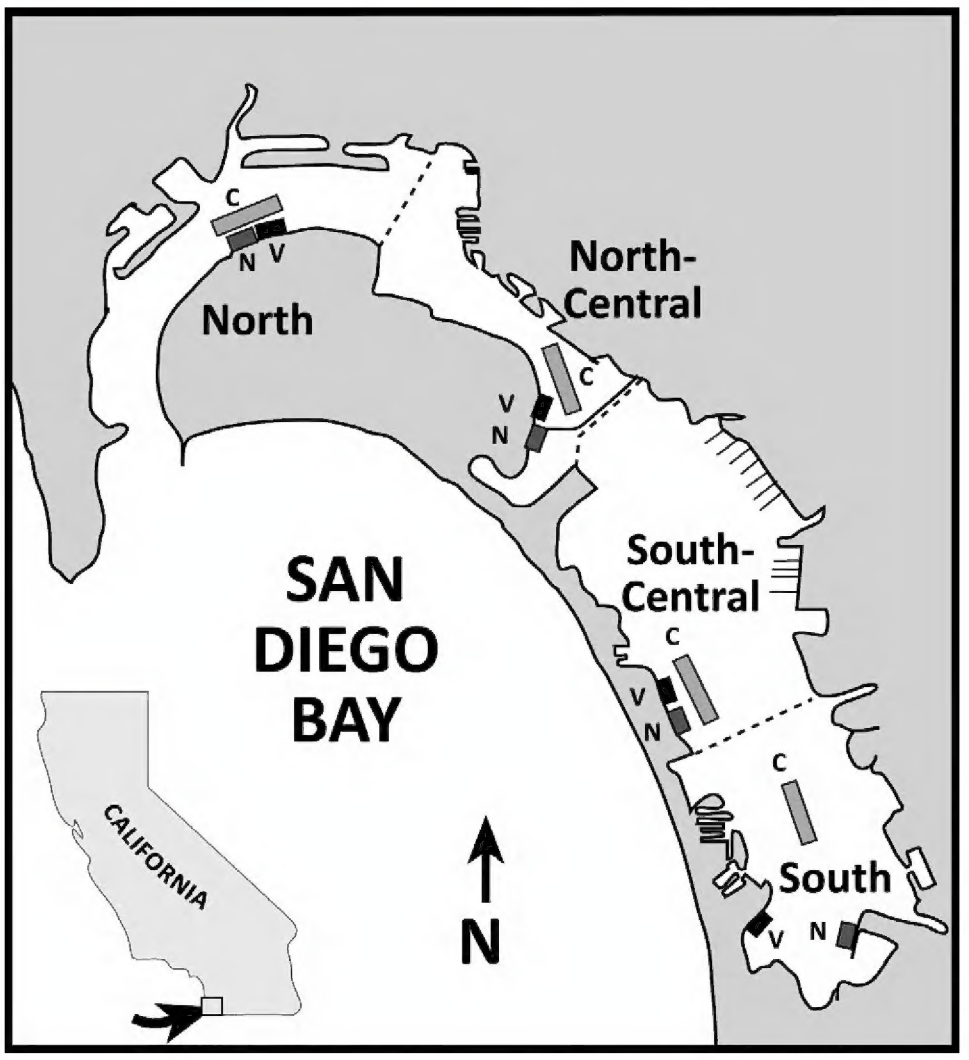

Fig. 1. Map of San Diego Bay illustrating the locations of the four ecoregions occupied in April and July for 11 years between 1995 and 2019 (N = non-vegetated sub-habitat; V = vegetated sub-habitat; C = channel sub-habitat).

resilient. The objective of the current study was to identify and quantify the fish populations in San Diego Bay over two and half decades of interrupted sampling in the months of April and July of the years 1995-1998, 2005, 2008, 2012, 2014-2016, and 2019. To these ends, the following were determined and will be described for the 25-year period, April 1995 to July 2019 in San Diego Bay: 1) spatial composition, numerical, and biomass abundance of the fish species, including forage fishes, 2) fish abundance patterns in relationship to bay physical and chemical factors including oceanographic indices, and 3) observed trends in species richness, composition, and diversity over time and in relation to eelgrass coverage. In a resilient system, we predict these metrics are maintained despite the environmental perturbations (Cote and Darling 2010).

Materials and Methods

To assess the status of all components of the ichthyofauna of San Diego Bay, we sampled intensively in each ecoregion (north, north-central, south-central, and south) of the bay (Fig. 1). Five sub-habitat types were sampled in each ecoregion: 1) channel, 2) nearshore, non-vegetated, 3) nearshore, vegetated, 4) intertidal, non-vegetated, and 5) intertidal vegetated. The actual sampling locations for each type of gear within each ecoregion sub-habitat were selected haphazardly for each sampling period (Allen et al. 2002). Sampling was conducted twice in each sampling year from April 1995 to July 2019, though sampling was not done every year. Each ecoregion was occupied on a separate day with a multiple

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gear approach, which was necessary to adequately sample all available fish habitat types. At each ecoregion, three replicates of each appropriate gear type were conducted in each sub-habitat. In the channel 8-m semi-balloon otter trawl (2-cm wing mesh 0.8-cm cod-end mesh, sample area of 2417 m^2) and a 66 × 6-m purse seine (1.2-cm wing mesh and 0.6-cm bag mesh, sample area of 296 m^2). Purse seines and 1.6-m beam trawls (4-mm wing mesh and 2-mm knotless cod-end mesh, sample area of 290 m^2) were conducted in the nearshore sub-habitats. In the intertidal habitats a 15.2 × 1.8-m large seine (1.8 × 1.8 × 1.8-m bag with 1.2-cm wing mesh and 0.6 cm bag mesh, sample area of 220 m^2), a 4.6 × 1.2-m small seine (3-mm mesh, sample area 62 m^2) and a square enclosure (1.0 × 1.0 × 1.0-m) with 1 liter of 3:1 acetone-rotenone solution. All fishes or subsamples of large catches were identified, counted, measured (standard length), and weighed in the field or in the laboratory after freezing, to the nearest 0.1 g on a digital scale. Physical and chemical measurements were taken once at each of the four ecoregions during each of the April and July sampling periods, where water temperature (°C) and salinity (‰) were measured at each ecoregion at the nearshore surface.

All analyses were performed using R version 4.1.2 (R Core Team 2021). As is common with ecological fish data, raw catch data were generally non-normal with unequal variances. Thus, all catch data for number of individuals for all species were log transformed before statistical comparisons were made. This transformation generally solved problems of normality and unequal variances in this data set. Bray-Curtis similarity and Shannon diversity (H') of all replicates pooled by sampling period were calculated using the 'vegdist' and 'diversity' functions, respectively, in the *vegan* package (Oksanen et al. 2020). Canonical correlation analysis examining the relationship between prominent physical and chemical factors such as temperature, salinity, and distance from the mouth of the bay and the abundance of each of the most frequently captured species were performed using the 'cc' function in the CCA package (González and Déjean 2021). Time-series analysis (trend analysis using the Seasonal Mann-Kendall statistic) was carried out using the 'Seasonal Mann-Kendall' function in the Kendall package (McLeod 2011). Forage species selected for analysis are defined herein as those which are accessible to diving avian predators, particularly terns. We further tested for correlations between any of the taxa with identified trends and composite oceanographic indices, including Pacific Decadal Oscillation (PDO), Oceanographic Nino Index (ONI), North Pacific Gyre Oscillation (NPGO), Multivariate ENSO Index (MEI), and Sea Surface Temperature (SST) from the Scripps Pier.

Results

Temperature varied from a high of 28.8°C at the south ecoregion in July 2014 to a low of 15.1°C in the north ecoregion in April 2012 (Fig. 2). The highest mean temperatures were encountered in the July sampling period each year and was the highest in the south ecoregion. The lowest temperatures were encountered in the April samplings. Thermal variability was evident during all sampling periods with temperatures becoming progressively warmer (2-6°C) north to south in the bay (Fig. 2). Surface salinity was relatively stable over the years of the study period varying about 8.5‰ (mean = 34.2‰) over the study period with both the highest (37.3‰ in July 1996 and 1997) and the lowest (28.8‰ in Apr 2012) values encountered in the south ecoregion. Mean salinities peaked in July of each sampled year when 35-37‰ prevailed at all ecoregions (Fig. 2). Overall, mean monthly salinities ranged from 31.6‰ (April 1998) to 36.0‰ (July 1996).

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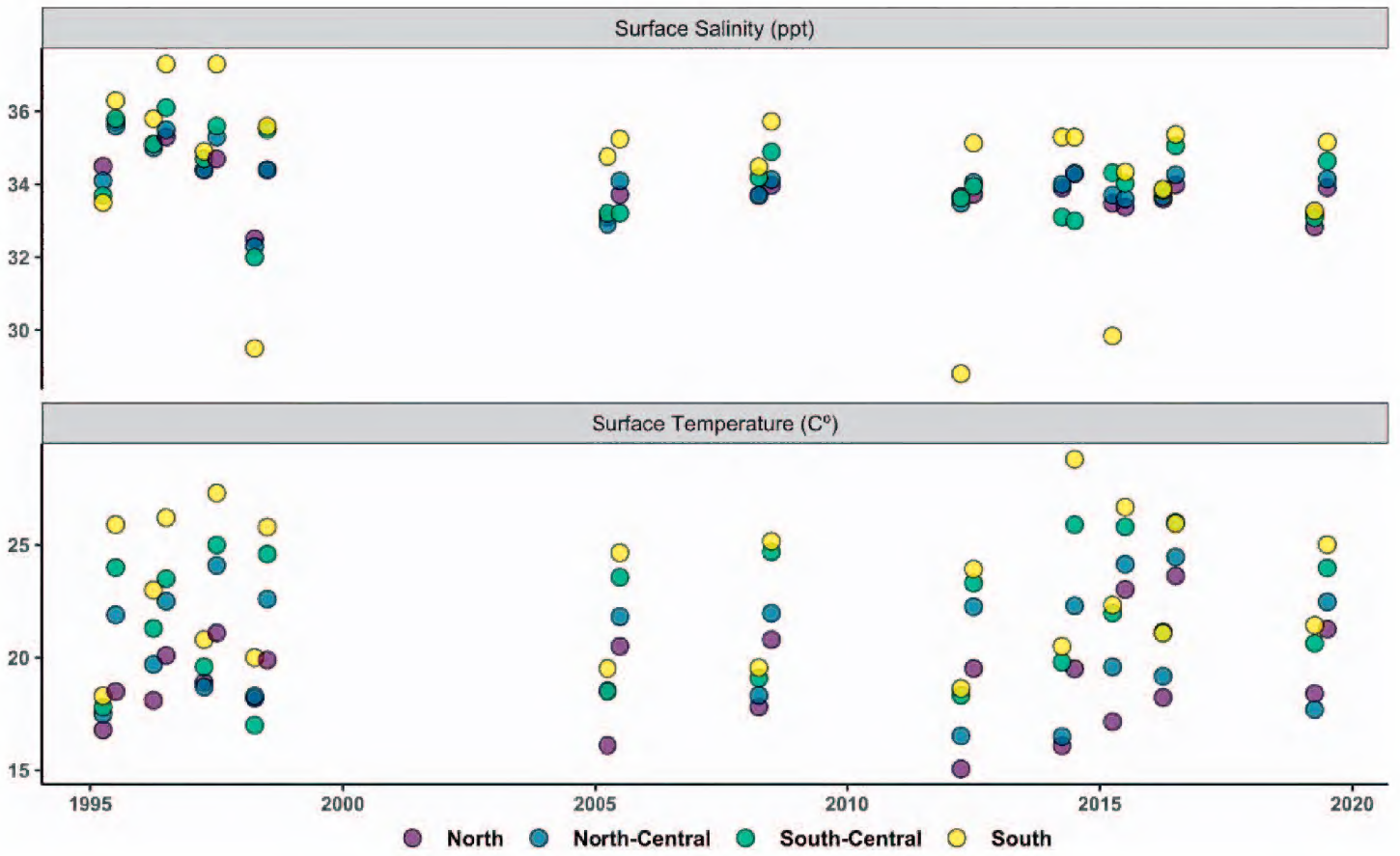

Fig. 2. Summary of Mean Surface Temperature (°C) and Salinity (‰) measurements by ecoregion over the sampling months, April 1995 to July 2019.

A total of 525,288 fishes belonging to 90 species and weighing 3,507 kg were captured in the 22 sampling efforts from April 1995 to July 2019 in San Diego Bay (Tables 1 and 2). Northern anchovy (*Engraulis mordax*) was the most abundant fish species comprising 41% of the total catch, followed by topsmelt at 23%, the slough anchovy at 21%, shiner surfperch at 3%, and Pacific sardine (*Sardinops sagax*) at about 2% of the total catch (Table 1). Round stingrays dominated in weight constituting approximately 27% of the total biomass taken, followed by spotted sand bass at about 14%, northern anchovy at approximately 9%, topsmelt at almost 8%, and slough anchovy and bat ray (*Myliobatis californica*) at 6% each (Table 2). Total abundance was variable over space and time with the largest catches in 1996 and the lowest in 2014 (Fig. 3). Similarly, biomass was also high in 1996 and lowest in 2008 (Fig. 4). The greatest number of individuals was taken at the north ecoregion (213,068) followed closely by north-central (194,995), then south-central (64,624), and the south ecoregion (52,601) (Table 1). The high count in the north and north-central ecoregions compared to the other ecoregions was primarily due to the large numbers of juvenile

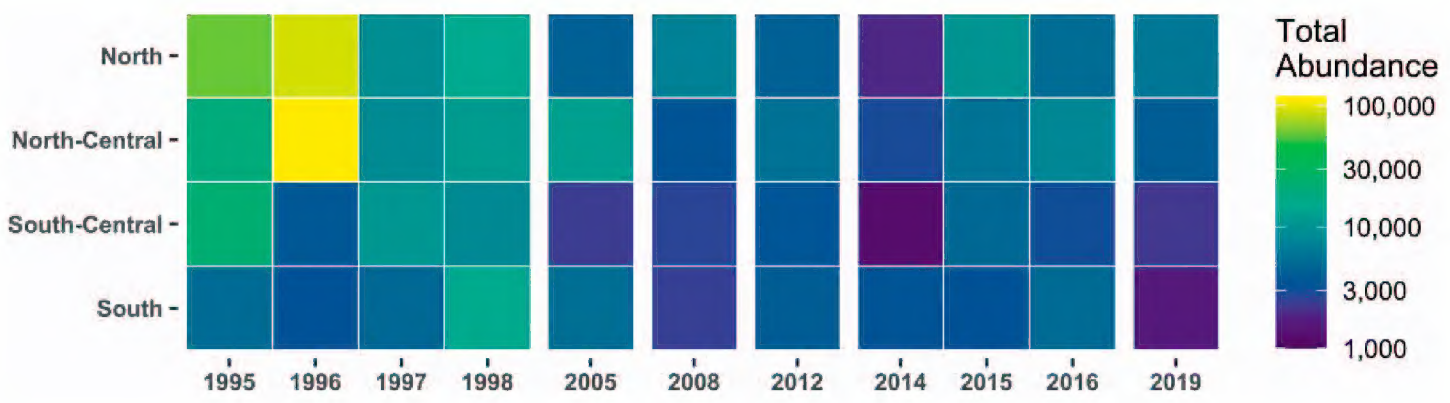

Fig. 3. Numerical abundance of San Diego Bay fishes by ecoregion, 1995-2019.

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Table 1. Total abundance of fish species taken from San Diego Bay over the 25-year period of the study, April 1995 to July 2019 by ecoregion.

Scientific name	Common name	North	North-central	South-central	South	Total	%
Engraulis mordax	northern anchovy	130,407	84,393	1,998	421	217,219	41.35
Atherinops affinis	topsmelt	46,429	51,367	11,592	9,427	118,815	22.62
Anchoa delicatissima	slough anchovy	7,473	37,832	35,069	28,346	108,720	20.7
Cymatogaster aggregata	shiner perch	3,743	5,411	5,974	2,435	17,563	3.34
Sardinops sagax	Pacific sardine	7,550	1,279	333	62	9,224	1.76
Heterostichus rostratus	giant kelpfish	2,981	4,551	1,236	198	8,966	1.71
Leuresthes tenuis	California grunion	5429	1,753	600	7	7,789	1.48
Clevelandia ios	arrow goby	832	533	871	4726	6,962	1.33
Syngnathus californiensis	kelp pipefish	843	1581	1930	1,224	5,578	1.06
Urobatis halleri	round stingray	807	1,440	1,244	1,805	5,296	1.01
Paralabrax maculatofasciatus	spotted sand bass	285	1169	911	634	2,999	0.57
Paralabrax nebulifer	barred sand bass	182	1,111	682	266	2,241	0.43
Micrometrus minimus	dwarf perch	1956	42	2	18	2,018	0.38
Anchoa compressa	deepbody anchovy	10	232	1153	554	1,949	0.37
Haemulon californiensis	salema	1,347	122	15	59	1,543	0.29
Syngnathus auliscus	barred pipefish	239	334	277	502	1,352	0.26
Paralichthys californicus	California halibut	307	215	188	169	879	0.17
Paralabrax clathratus	kelp bass	335	122	15	5	477	0.09
Hypsoblennius gentilis	bay blenny	90	314	43	4	451	0.09
Fundulus parvipinnis	California killifish		8	38	377	423	0.08
Embiotoca jacksoni	black perch	378	34			412	0.08
Atherinopsis californiensis	jacksmelt	32	80	3	264	379	0.07
Ilypnus gilberti	cheekspot goby	65	49	39	149	302	0.06
Pleuronichthys guttulatus	diamond turbot	77	64	66	91	298	0.06
Symphurus atricaudus	California tonguefish	219	29	3		251	0.05
Seriphus politus	queenfish	177	54	10	3	244	0.05
Quietula y-cauda	shadow goby	21	123	5	88	237	0.05
Mugil cephalus	striped mullet				236	236	0.04
Albula gilberti	Cortez bonefish	5	130	22	78	235	0.04
Porichthys myriaster	specklefin midshipman	84	43	31	49	207	0.04
Cheilotrema saturnum	black croaker	47	68	35	33	183	0.03
Leptocottus armatus	Pacific staghorn sculpin	22	66	44	44	176	0.03
Pleuronichthys ritteri	spotted turbot	92	74	6	3	175	0.03
Scomber japonicus	Pacific chub mackerel	24	97	20		141	0.03
Phanerodon furcatus	white seaperch	73	50	5		128	0.02

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Table 1. Continued

Scientific name	Common name	North	North-central	South-central	South	Total	%
Gibbonsia elegans	spotted kelpfish	74	42	4	5	125	0.02
Hyporhamphus rosae	California halfbeak	2	2	28	91	123	0.02
Synodus lucioceps	California lizardfish	86	13	4	6	109	0.02
Umbrina roncador	yellowfin croaker		15	29	35	79	0.02
Citharichthys stigmaeus	speckled sanddab	64	4		1	69	0.01
Halichoeres semicinctus	rock wrasse	64	2			66	0.01
Sphyraena argentea	Pacific barracuda	12	10		43	65	0.01
Myliobatis californica	bat ray	1	12	17	32	62	0.01
Cynoscion parvipinnis	shortfin corvina	6	20	21	8	55	0.01
Scorpaena guttata	California scorpionfish	27	5	1		33	0.01
Xystreurys liolepis	fantail sole	26	3		1	30	0.01
Gymnura marmorata	California butterfly ray	1	3	4	20	28	0.01
Acanthogobius flavimanus	yellowfin goby	1	1	3	22	27	0.01
Pleuronichthys decurrens	curlfin sole	18	8	1		27	0.01
Cosmocampus arctus	snubnose pipefish	7	17	2		26	<0.01
Strongylura exilis	California needlefish	4	7	7	5	23	<0.01
Trachurus symmetricus	jack mackerel	19	2		1	22	<0.01
Oxyjulis californica	señorita	20				20	<0.01
Hypsoblennius jenkinsi	mussel blenny	2	10	6	1	19	<0.01
Tridentiger trigonocephalus	chameleon goby		6	10	3	19	<0.01
Gillichthys mirabilis	longjaw mudsucker			1	17	18	<0.01
Hippocampus ingens	Pacific seahorse	1	4	7	6	18	<0.01
Atractoscion nobilis	white seabass	6	3	2	6	17	<0.01
Roncador stearnsii	spotfin croaker		8	4	4	16	<0.01
Genyonemus lineatus	white croaker	13	1	1		15	<0.01
Hyperprosopon anale	spotfin surfperch	8	2			10	<0.01
Heterodontus francisci	horn shark	6	2	1		9	<0.01
Anisotremus davidsonii	sargo		5	1	2	8	<0.01
Girella nigricans	opaleye	7				7	<0.01
Mustelus californicus	gray smoothhound		1		6	7	<0.01
Zapteryx exasperata	banded guitarfish	7				7	<0.01
Rhacochilus vacca	pile perch	6				6	<0.01
Brachyistius frenatus	kelp perch		5			5	<0.01
Menticirrhus undulatus	California corbina		4	1		5	<0.01
Ctenogobius sagittula	longtail goby				4	4	<0.01
Gibbonsia metzi	striped kelpfish	3	1			4	<0.01
Platyrhinoidis triseriata	thornback	4				4	<0.01

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Table 1. Continued

Scientific name	Common name	North	North-central	South-central	South	Total	%
Rhinobatos productus	shovelnose guitarfish			2	2	4	<0.01
Sarda chiliensis	Pacific bonito			4		4	<0.01
Hypsurus caryi	rainbow seaperch		3			3	<0.01
Paraclinus integripinnis	reef finspot	1		2		3	<0.01
Porichthys notatus	plainfin midshipman	1			2	3	<0.01
Dasyatis dipterura	diamond stingray		1		1	2	<0.01
Pleuronichthys verticalis	hornyhead turbot	1	1			2	<0.01
Squatina californica	Pacific angel shark	1	1			2	<0.01
Alloclinus holderi	island kelpfish	1				1	<0.01
Hippoglossina stomata	bigmouth sole		1			1	<0.01
Hyperprosopon argenteum	walleye surfperch	1				1	<0.01
Medialuna californiensis	halfmoon	1				1	<0.01
Mustelus henlei	brown smoothhound			1		1	<0.01
Pleuronichthys coenosus	c-o sole	1				1	<0.01
Pseudupeneus grandisquamis	bigscale goatfish	1				1	<0.01
Rimicola muscarum	kelp clingfish	1				1	<0.01
Sebastes rastrelliger	grass rockfish	1				1	<0.01
Sebastes serranoides	olive rockfish	1				1	<0.01
Total		**213,068**	**194,995**	**64,624**	**52,601**	**525,288**	
Number of Species		**73**	**69**	**59**	**56**	**90**	

northern anchovy, topsmelt, and Pacific sardine taken at these ecoregions in two years (1995, 1996), mostly by purse seine (Table 3). This pattern of abundance was the opposite for the slough anchovy, which was prominent in the southern portion of the bay, and shiner surfperch was most common in the central portions of the bay (Table 1).

The pattern for biomass was similarly highest in the northern ecoregions compared to the southern ecoregions. Large catches of round stingray and spotted sand bass were taken across all ecoregions and the variation in their catch, coupled with large catches of northern

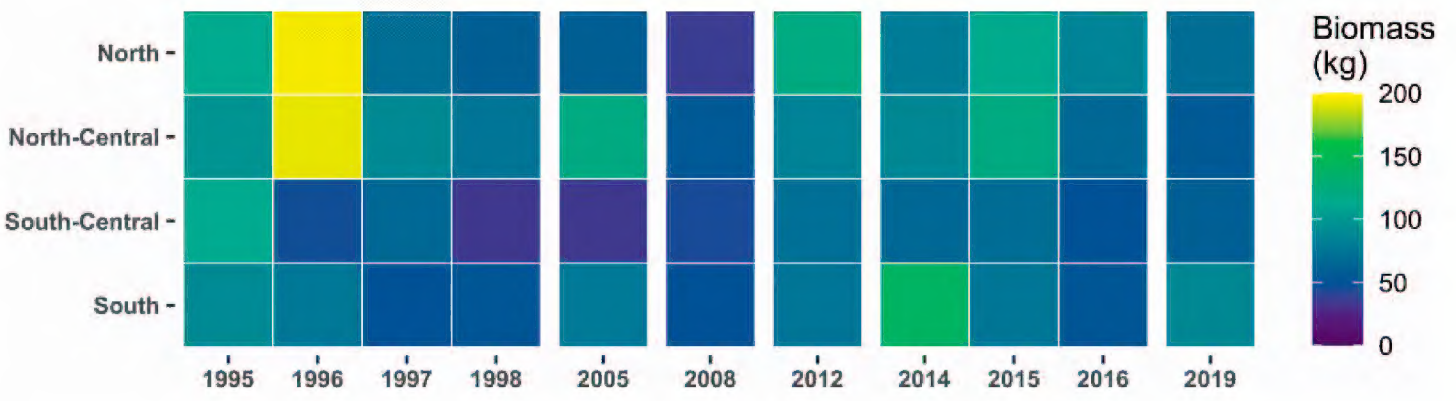

Fig. 4. Biomass (g) of San Diego Bay Fishes by Ecoregion, 1995-2019.

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Table 2. Total biomass (g) of fish species taken from San Diego Bay over the 25-year period of the study, April 1995 to July 2019 by ecoregion.

Scientific name	Common name	North	North-central	South-central	South	Total	%
Urobatis halleri	round stingray	224,055	251,679	196,082	286,725	958,541	27.33
Paralabrax maculatofasciatus	spotted sand bass	75,266	201,698	111,121	109,496	497,580	14.19
Engraulis mordax	northern anchovy	219,568	98,978	1,639	822	321,007	9.153
Atherinops affinis	topsmelt	140,536	94,193	18,116	24,525	277,369	7.91
Anchoa delicatissima	slough anchovy	19,459	85,928	73,281	43,763	222,430	6.34
Myliobatis californica	bat ray	10,000	54,810	92,461	62,601	219,872	6.27
Paralabrax nebulifer	barred sand bass	19,092	37,515	17,490	45,624	119,721	3.41
Sardinops sagax	Pacific sardine	24,428	5,728	1,108	86,040	117,304	3.34
Cymatogaster aggregata	shiner perch	28,599	40,147	25,707	6,882	101,335	2.89
Paralichthys californicus	California halibut	43,516	22,297	13,489	11,676	90,978	2.59
Gymnura marmorata	California butterfly ray	7,500	1,808	9,100	70,644	89,052	2.54
Leuresthes tenuis	California grunion	21,420	11,782	10,007	1.0	43,210	1.23
Heterostichus rostratus	giant kelpfish	15,800	15,833	5,975	1,210	38,817	1.11
Pleuronichthys guttulatus	diamond turbot	14,196	10,591	3,076	3,568	31,430	0.90
Anchoa compressa	deepbody anchovy	142	746	16,605	8,846	26,338	0.75
Cynoscion parvipinnis	shortfin corvina	5,714	13,005	6,376	766	25,861	0.74
Scomber japonicus	Pacific chub mackerel	5,160	11,472	3,307		19,939	0.57
Cheilotrema saturnum	black croaker	4,625	5,168	4,248	4,717	18,758	0.53
Roncador stearnsii	spotfin croaker		7,800	5,500	4,500	17,800	0.51
Umbrina roncador	yellowfin croaker		5,136	4,982	7,549	17,666	0.50
Squatina californica	Pacific angel shark	5,000	12,000			17,000	0.48
Embiotoca jacksoni	black perch	15,349	1,560			16,909	0.48
Micrometrus minimus	dwarf perch	14,737	489	10	86	15,323	0.44
Albula gilberti	Cortez bonefish	2	653	6,759	6,559	13,973	0.40
Pleuronichthys ritteri	spotted turbot	6,855	6,261	152	77	13,345	0.38
Haemulon californiensis	salema	8,774	2,969	270	804	12,816	0.37
Rhinobatos productus	shovelnose guitarfish			6,595	5,800	12,395	0.35
Porichthys myriaster	specklefin midshipman	4,552	3,244	3,004	1,193	11,992	0.34
Paralabrax clathratus	kelp bass	7,000	1,963	323	151	9,437	0.27
Dasyatis dipterura	diamond stingray		5,000		4,200	9,200	0.26
Atherinopsis californiensis	jacksmelt	2,726	2,008	83	3,755	8,573	0.24
Seriphus politus	queenfish	6,113	1,467	576	198	8,354	0.24
Scorpaena guttata	California scorpionfish	7,233	738	95		8,066	0.23
Mustelus californicus	gray smoothhound		968		6,815	7,783	0.22
Atractoscion nobilis	white seabass	2,019	1,870	292	2,148	6,329	0.18

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Table 2. Continued

Scientific name	Common name	North	North-central	South-central	South	Total	%
Menticirrhus undulatus	California corbina		3,860	2,450		6,310	0.18
Heterodontus francisci	horn shark	3,062	3,220	4		6,286	0.18
Sphyraena argentea	Pacific barracuda	1,112	1,559		3,115	5,786	0.16
Xystreurys liolepis	fantail sole	3,767	1,456		188	5,411	0.15
Trachurus symmetricus	jack mackerel	4,245	260		240	4,745	0.14
Hypsoblennius gentilis	bay blenny	840	2,930	623	104	4,497	0.13
Anisotremus davidsonii	sargo		3,726	579	184	4,489	0.13
Platyrhinoidis triseriata	thornback	4,300				4,300	0.12
Synodus lucioceps	California lizardfish	3,194	663	118	101	4,075	0.12
Syngnathus californiensis	kelp pipefish	1,172	1,156	1,002	567	3,898	0.11
Halichoeres semicinctus	rock wrasse	2,743	130			2,874	0.08
Sarda chiliensis	Pacific bonito			2,700		2,700	0.08
Zapteryx exasperata	banded guitarfish	2,588				2,588	0.07
Symphurus atricaudus	California tonguefish	1,940	392	55		2,387	0.07
Strongylura exilis	California needlefish	184	992	403	619	2,198	0.06
Girella nigricans	opaleye	2,157				2,157	0.06
Mugil cephalus	striped mullet				1,826	1,826	0.05
Phanerodon furcatus	white seaperch	1,262	393	8		1,663	0.05
Clevelandia ios	arrow goby	116	69	891	571	1,646	0.05
Leptocottus armatus	Pacific staghorn sculpin	235	483	457	315	1,490	0.04
Pleuronichthys decurrens	curlfin sole	763	178	35		976	0.03
Syngnathus auliscus	barred pipefish	226	174	269	277	945	0.03
Gibbonsia elegans	spotted kelpfish	461	392	11	10	874	0.02
Fundulus parvipinnis	California killifish		65	221	562	848	0.02
Mustelus henlei	brown smoothhound			813		813	0.02
Genyonemus lineatus	white croaker	610	100	17		727	0.02
Oxyjulis californica	señorita	664				664	0.02
Hippocampus ingens	Pacific seahorse	15	168	243	199	624	0.02
Citharichthys stigmaeus	speckled sanddab	483	33		3	519	0.01
Hyporhamphus rosae	California halfbeak	1.1	6	243	203	453	0.01
Rhacochilus vacca	pile perch	400				400	0.01
Hypsoblennius jenkinsi	mussel blenny	14	170	125	30	339	0.01
Acanthogobius flavimanus	yellowfin goby	3	12	41	185	242	0.01
Pleuronichthys coenosus	c-o sole	121				121	<0.01
Hyperprosopon anale	spotfin surfperch	69	35			104	<0.01
Pseudupeneus grandisquamis	bigscale goatfish	100				100	<0.01

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Table 2. Continued

Scientific name	Common name	North	North-central	South-central	South	Total	%
Ilypnus gilberti	cheekspot goby	5	7	9	74	96	<0.01
Ctenogobius sagittula	longtail goby				70	70	<0.01
Hyperprosopon argenteum	walleye surfperch	59				59	<0.01
Quietula y-cauda	shadow goby	11	15	1.0	29	56	<0.01
Pleuronichthys verticalis	hornyhead turbot	6	45			51	<0.01
Gillichthys mirabilis	longjaw mudsucker			9	31	40	<0.01
Brachyistius frenatus	kelp perch		31			31	<0.01
Hypsurus caryi	rainbow seaperch		20			20	<0.01
Tridentiger trigonocephalus	chameleon goby		2	5	4	11	<0.01
Cosmocampus arctus	snubnose pipefish	2	6	2		10	<0.01
Paraclinus integripinnis	reef finspot	3		2		5	<0.01
Hippoglossina stomata	bigmouth sole		5			5	<0.01
Gibbonsia metzi	striped kelpfish	3	0.3			4	<0.01
Sebastes serranoides	olive rockfish	3				3	<0.01
Sebastes rastrelliger	grass rockfish	3				3	<0.01
Porichthys notatus	plainfin midshipman	0.2			1.1	1.3	<0.01
Alloclinus holderi	island kelpfish	0.6				0.6	<0.01
Medialuna californiensis	halfmoon	0.4				0.4	<0.01
Rimicola muscarum	kelp clingfish	0.2				0.2	<0.01
Total		**996,380**	**1,040,258**	**649,160**	**821,246**	**3,507,044**	

Table 3. Abundance of the ten most frequently caught fish species taken from San Diego Bay over the 25-year period of the study, April 1995 to July 2019 by sampling method.

Scientific name	Common	Purse seine	Otter trawl	Beam trawl	Large seine	Small seine	Square enclosure
Engraulis mordax	northern anchovy	215,663	502	8	613	433	
Atherinops affinis	topsmelt	25,536	9	98	31,315	61,446	411
Anchoa delicatissima	slough anchovy	97,869	2,072	1,426	6,533	820	
Cymatogaster aggregata	shiner perch	12,565	116	3,694	1,135	52	1
Sardinops sagax	Pacific sardine	9,219	5				
Heterostichus rostratus	giant kelpfish	962	4	7,270	650	75	5
Leuresthes tenuis	California grunion	4,995			819	1,974	1
Clevelandia ios	arrow goby	1	14	1,653	587	4,327	380
Syngnathus californiensis	kelp pipefish	55	33	4,590	328	565	7
Urobatis halleri	round stingray	1,249	2,404	1,481	144	18	

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Table 4. Biomass (g) of the ten fish species with the highest overall biomass taken from San Diego Bay over the 25-year period of the study, April 1995 to July 2019 by sampling method.

Scientific name	Common	Purse seine	Otter trawl	Beam trawl	Large seine	Small seine	Square enclosure
Urobatis halleri	round stingray	255,598	401,678	270,512	28,024	2,730	
Paralabrax maculatofasciatus	spotted sand bass	309,722	83,102	100,138	4,393	158	67
Engraulis mordax	northern anchovy	318,981	834	12	1,038	143	
Atherinops affinis	topsmelt	205,062	278	271	59,413	12,317	27
Anchoa delicatissima	slough anchovy	209,713	2,534	999	8,713	471	
Myliobatis californica	bat ray	191,599	9,793	6,250	11,540	690	
Paralabrax nebulifer	barred sand bass	9,774	89,476	16,267	4,078	126	
Sardinops sagax	Pacific sardine	117,210	94				
Cymatogaster aggregata	shiner perch	82,937	1,080	11,774	5,319	205	20
Paralichthys californicus	California halibut	20,339	58,367	10,385	1,838	46	3

anchovies captured by purse seine (Table 4) in the north and north-central ecoregions, drove the general pattern of higher biomass in the northern half of the bay. Overall, species composition and abundance among the 11 sampling years included in this study varied little sharing a high mean percent similarity of 78 ± 4.7% (Table 5). Approximately 64% of all individual fish captured in San Diego Bay during this study were juveniles. In fact, 26 of the 35 most abundant species were represented by over 50% juveniles (Table 6), and of these, eight species were represented by more than 90% juveniles.

Canonical correlation was utilized to estimate the relationship of the three prominent physical and chemical factors (distance from the mouth of the bay, temperature, and salinity) to individual ecoregion abundances of the 35 most abundant species. These three factors accounted for nearly 92.5% of the variance in individual species abundance among ecoregions over sampling months of the sampled years (Table 7). This high value served to

Table 5. Percent similarity of the top 35 fish species among years over the 25-year study period.

YEAR	1995	1996	1997	1998	2005	2008	2012	2014	2015	2016	2019
1995											
1996	89										
1997	82	84					**Average**		78		
1998	76	81	79				**STD**		4.7		
2005	78	77	77	73							
2008	79	74	78	66	81						
2012	77	74	73	65	81	85					
2014	75	73	72	67	79	80	80				
2015	80	82	77	75	86	81	79	80			
2016	77	76	79	76	82	80	77	76	87		
2019	76	74	77	67	77	79	81	82	79	78	

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Table 6. Estimated percent of juveniles in the catch of the top 35 species of fish from San Diego Bay, April 1995-July 2015.

Scientific name	Common name	% Juveniles
Haemulon californiensis	salema	99.7
Paralabrax clathratus	kelp bass	99.5
Paralabrax nebulifer	barred sand bass	99.5
Heterostichus rostratus	giant kelpfish	98.9
Citharichthys stigmaeus	speckled sanddab	98.5
Phanerodon furcatus	white seaperch	97.6
Paralichthys californicus	California halibut	94.5
Gibbonsia elegans	spotted kelpfish	91.5
Symphurus atricaudus	California tonguefish	86.8
Leuresthes tenuis	California grunion	84.3
Engraulis mordax	northern anchovy	83.1
Atherinopsis californiensis	jacksmelt	81.6
Embiotoca jacksoni	black perch	80.0
Porichthys myriaster	specklefin midshipman	77.3
Urobatis halleri	round stingray	75.0
Syngnathus californiensis	kelp pipefish	74.8
Albula gilberti	Cortez bonefish	72.1
Cymatogaster aggregata	shiner perch	71.9
Atherinops affinis	topsmelt	67.7
Halichoeres semicinctus	rock wrasse	67.7
Syngnathus leptorhynchus	bay pipefish	65.2
Leptocottus armatus	Pacific staghorn sculpin	64.8
Micrometrus minimus	dwarf perch	60.9
Fundulus parvipinnis	California killifish	59.8
Clevelandia ios	arrow goby	57.7
Pleuronichthys guttulatus	diamond turbot	55.4
Paralabrax maculatofasciatus	spotted sand bass	38.1
Ilypnus gilberti	cheekspot goby	25.3
Pleuronichthys ritteri	spotted turbot	24.7
Hyporhamphus rosae	California halfbeak	20.6
Hypsoblennius gentilis	bay blenny	20.1
Anchoa delicatissima	slough anchovy	19.0
Sardinops sagax	Pacific sardine	17.1
Sphyraena argentea	Pacific barracuda	15.9
Anchoa compressa	deepbody anchovy	5.5
Average % juveniles		64.3

underscore the great influence which relatively few environmental factors can have on the distribution and abundance of the 35 most abundant fishes over time (Fig. 5).

Time-series analysis yielded all potential patterns of variation for abundance, biomass, and diversity (Table 8). Neither total abundance of all species combined ($p = 0.099$), total biomass ($p = 0.826$), Shannon diversity ($p = 0.078$) nor species richness ($p = 0.503$) changed significantly over time (Fig. 6 and 7). Eight species among the top 35 most abundant significantly decreased in abundance over time (Table 8). Northern anchovy ($p = 0.016$), topsmelt ($p = 0.003$), slough anchovy ($p = 0.036$), and shiner perch ($p < 0.001$) were amongst those forage species that exhibited significant decreases over time (Fig. 8). Pacific sardine abundance also decreased over time, but the decreases were not significant ($p = 0.310$) due to high variability. When considered together as a group of important forage fishes in San Diego Bay, these five abundant species decreased significantly over time

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Table 7. Results of canonical correlation analysis for three physical and chemical factors (Distance from mouth of bay (km), Temperature, and Salinity) versus log10-abundance of the 35 most abundant individual species taken at each ecoregion in sampling from San Diego Bay, April 1995 – July 2019.

Wilks' Lambda, using F-approximation (Rao's F)				
Root removed	Canonical R^2	F	df	p
0	0.925	5.656	105, 150.6	<0.001
1	0.714	2.946	68, 102	<0.001
2	0.602	2.393	33, 52	0.002

Standardized canonical weights, physical-chemical factors			
Variable	Dimension 1	Dimension 2	Dimension 3
Temperature (°C)	0.212	−0.373	1.247
Salinity (ppt)	−0.017	−0.804	−0.814
Distance (km)	0.878	0.392	−0.674

($p = 0.004$) (Fig. 8). Additionally, four less-abundant species, barred pipefish, cheekspot goby, shadow goby, and black croaker (*Cheilotrema saturnum*), also exhibited significant declines (Table 8), though the most likely explanation for the decrease in barred pipefish is misidentification as it can be difficult to discern between pipefish congeners.

Two species showed significant increases over the course of the study. Spotted sand bass increased significantly ($p = 0.001$) in numerical abundance from 1995 to 2019 but showed no change in biomass ($p = 0.322$) (Fig. 9). The second species that increased in abundance was the dwarf perch (*Micrometrus minimus*) that was present early in the sampling period, became rare to absent, then increased in abundance from 2008 to 2019 ($p = 0.012$). Lastly, no significant correlations were found among the composite oceanographic indices with any of the identified trends in fish species abundance, total abundance, species richness, H' diversity, or biomass trends.

Discussion

A total of 90 fish species was identified during the 25 years of monitoring in San Diego Bay, a count similar to the predicted number (89) by the species-area relationship developed by Horn and Allen (1976), indicating that the fish assemblage remains intact despite human disturbances in the bay. Species richness by ecoregion in San Diego Bay was comparable, if not higher, than values obtained from other southern California bays, estuaries, and harbors. The north and north-central ecoregions of San Diego Bay (73 and 69 species, respectively) had similar species richness to multiple-gear sampling studies in Los Angeles Harbor and Newport Bay. Allen et al. (1983) captured 65 fish species in the Cabrillo Beach area of western Los Angeles Harbor in 1979. Allen (1976) sampled a total of 65 species from Newport Bay in 1974-75 in a sampling strategy that included stations from throughout the upper and lower bay. The south-central and south ecoregions yielded higher species richness (59 and 56 species, respectively) than comparable studies in other bay/estuaries in southern California. Onuf and Quammen (1983) caught a total of only 28 fish species when using a large beach seine capable of sampling most of the small, shallow embayment of Mugu Lagoon. Horn and Allen (1981) reported 46 species captured in a comparable,

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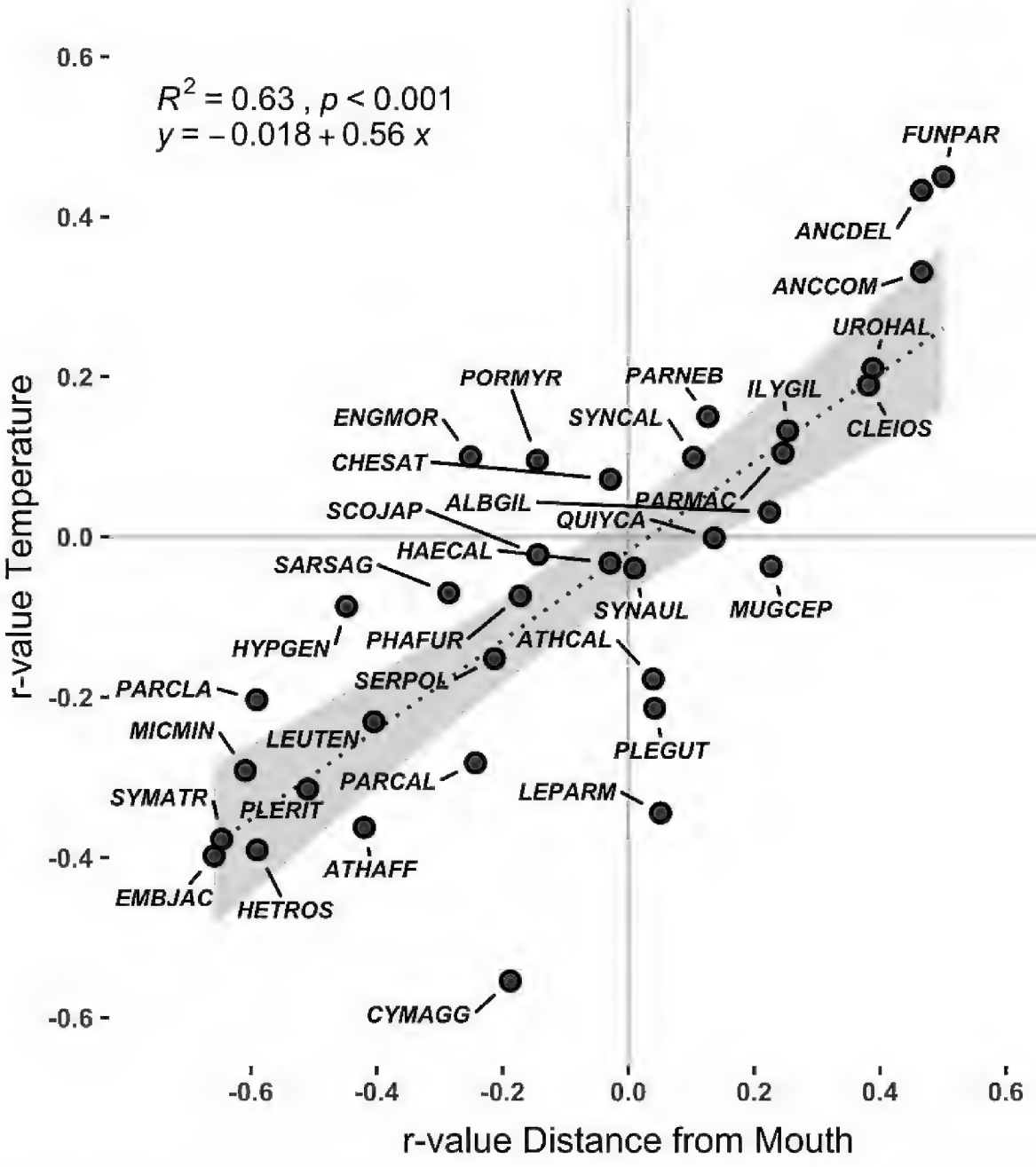

Fig. 5. Ordination of 35 most abundant fishes in San Diego Bay based on correlation coefficients (r) for distance from mouth of bay (x-axis) and temperature (y-axis). Dashed line and gray shading illustrate the regression line and 95% confidence intervals. ALBGIL = Cortez bonefish, ANCCOM = deepbody anchovy, ANCDEL = slough anchovy, ATHAFF = topsmelt, ATHCAL = jacksmelt, CHESAT = black croaker, CLEIOS = arrow goby, CYMAGG = shiner perch, EMBJAC = black perch, ENGMOR = northern anchovy, FUNPAR = California killifish, HAECAL = salema, HETROS = giant kelpfish, HYPGEN = bay blenny, ILYGIL = cheekspot goby, LEPARM = Pacific staghorn sculpin, LEUTEN = California grunion, MICMIN = dwarf perch, MUGCEP = striped mullet, PARCAL = California halibut, PARCLA = kelp bass, PARMAC = spotted sand bass, PARNEB = barred sand bass, PLEGUT = diamond turbot, PLERIT = spotted turbot, PHAFUR = white seaperch, PORMYR = specklefin midshipman, QUIYCA = shadow goby, SARSAG = Pacific sardine, SCOJAP = Pacific mackerel, SERPOL = queenfish, SYMATR = California tonguefish, SYNAUL = barred pipefish, SYNCAL = kelp pipefish, UROHAL = round stingray.

multiple-gear sampling design in upper Newport Bay in 1978. Furthermore, Allen (1988) reported 41 species from upper Newport Bay in 1986-1987.

As was found in a long-term survey (1987-2010) of intertidal fishes in San Diego Bay (Obaza et al. 2015), the fish assemblage structure across all sub-habitats of the bay remained consistent over the period of 1995 to 2019 and represents a blend of those fishes normally associated with harbors and bay/estuaries within the Southern California Bight (Allen and Pondella 2006). Allen et al. (2002) found that the northern ecoregions cluster with the fish assemblages from previous, comparable studies in southern California harbors

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Table 8. Results of time series analysis for the 35 most abundant species and total abundance and biomass sampled over the 25-year period of April 1995 to July 2019 in San Diego Bay by the trend analysis using the Mann-Kendall statistic and tau (∗ $p < 0.05$; ∗∗ $p < 0.01$).

Scientific name	Common name	Mann-Kendall statistic	tau	p	
Engraulis mordax	northern anchovy	−43	−0.408	0.016	∗
Atherinops affinis	topsmelt	−54	−0.491	0.003	∗∗
Anchoa delicatissima	slough anchovy	−38	−0.345	0.036	∗
Cymatogaster aggregata	shiner perch	−68	−0.618	<0.001	∗∗
Sardinops sagax	Pacific sardine	−18	−0.173	0.310	
Heterostichus rostratus	giant kelpfish	−8	−0.073	0.660	
Leuresthes tenuis	California grunion	−3	−0.031	0.859	
Clevelandia ios	arrow goby	8	0.073	0.660	
Syngnathus californiensis	kelp pipefish	34	0.309	0.061	
Urobatis halleri	round stingray	26	0.236	0.152	
Paralabrax maculatofasciatus	spotted sand bass	58	0.527	0.001	∗∗
Paralabrax nebulifer	barred sand bass	−30	−0.275	0.098	
Micrometrus minimus	dwarf perch	45	0.419	0.012	∗
Anchoa compressa	deepbody anchovy	21	0.194	0.245	
Haemulon californiensis	salema	9	0.097	0.583	
Syngnathus auliscus	barred pipefish	−64	−0.740	<0.001	∗∗
Paralichthys californicus	California halibut	−13	−0.120	0.472	
Paralabrax clathratus	kelp bass	15	0.137	0.408	
Hypsoblennius gentilis	bay blenny	−6	−0.055	0.740	
Fundulus parvipinnis	California killifish	−24	−0.231	0.176	
Embiotoca jacksoni	black perch	−30	−0.278	0.097	
Atherinopsis californiensis	jacksmelt	−1	−0.010	0.953	
Ilypnus gilberti	cheekspot goby	−47	−0.437	0.009	∗∗
Pleuronichthys guttulatus	diamond turbot	−22	−0.204	0.223	
Symphurus atricaudus	California tonguefish	−18	−0.168	0.317	
Seriphus politus	queenfish	0	0.000	1.000	
Quietula y-cauda	shadow goby	−39	−0.378	0.027	∗
Mugil cephalus	striped mullet	−23	−0.348	0.069	
Albula gilberti	Cortez bonefish	30	0.298	0.085	
Porichthys myriaster	specklefin midshipman	12	0.112	0.505	
Cheilotrema saturnum	black croaker	−50	−0.467	0.005	∗∗
Leptocottus armatus	Pacific staghorn sculpin	6	0.058	0.734	
Pleuronichthys ritteri	spotted turbot	−29	−0.270	0.107	
Scomber japonicus	Pacific chub mackerel	−15	−0.183	0.312	
Phanerodon furcatus	white seaperch	4	0.047	0.796	
	Total abundance	−30	−0.273	0.099	
	Forage species	−52	−0.473	0.004	∗∗
	Total biomass	−4	−0.036	0.826	
	Diversity (H')	32	0.291	0.078	
	Species richness	−12	−0.113	0.503	

while the southern ecoregions of San Diego Bay are more closely associated with the assemblages in the bay/estuaries of southern California. Therefore, San Diego Bay represents a large, unique environment within the Southern California Bight combining elements of two major types of habitats, namely harbor-nearshore soft bottom and bay/estuary (Allen and Pondella 2006). Additionally, as indicated by the high proportion of juveniles overall in the catch, the San Diego Bay system functions as an important nursery area for many fish species.

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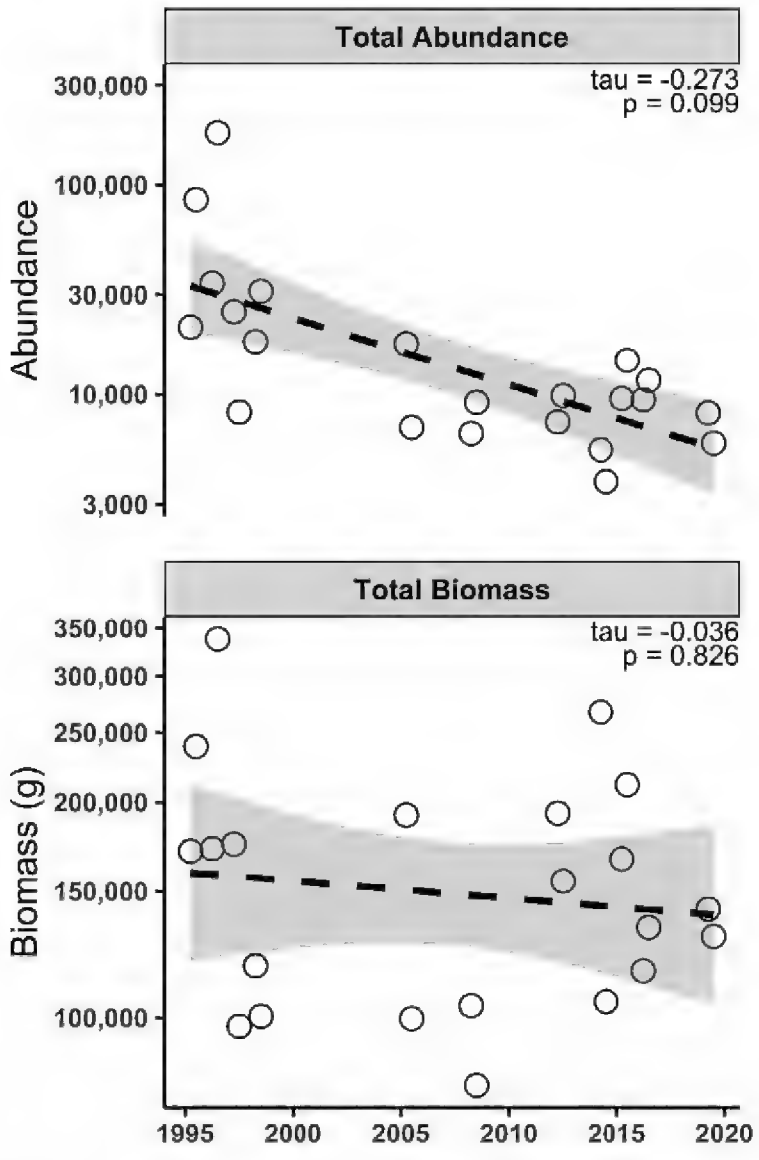

Fig. 6. Total abundance (top) and biomass (bottom) of all species combined by sample month over the interrupted time series in San Diego Bay from April 1995 to July 2019. Dashed line and gray shading illustrate the linear regression line of log-transformed abundance and biomass and 95% confidence intervals.

Our time series analysis identified some important trends in San Diego Bay. The patterns of overall decrease in abundance of eight of the 35 most abundant species, including several forage fish species, are similar to those reported in other fish population studies in southern California waters (Miller and McGowan 2013; Koslow et al. 2015) over roughly the same time period. Miller and McGowan (2013) reported coastal fish abundance indices over a 39-year (1972-2010) time series recorded at southern California coastal power plants where annual mean abundance index significantly declined over time and the annual entrapment rate abundance index during the period of 1990-2010 represented only 22% of that recorded during the 1972-1983 period. Consistent with our findings from 1995 to 2019, their declining trends were not correlated with the Pacific Decadal Oscillation or other composite climate indices but did suggest declines were somewhat driven by changes in coastal seawater temperature and density over time.

Koslow et al. (2015) compared the California Cooperative Oceanic Fisheries Investigations (CalCOFI) ichthyoplankton surveys with the aforementioned systematic sampling of southern California power plant cooling-water intakes. Their effort provided independent, complementary time series to assess fish communities off southern California from nearshore to oceanic environments. They reported that although there was limited overlap in the taxa sampled by the two programs, key multivariate patterns were highly correlated between the studies. Both efforts recorded a dramatic decline in abundance over time from

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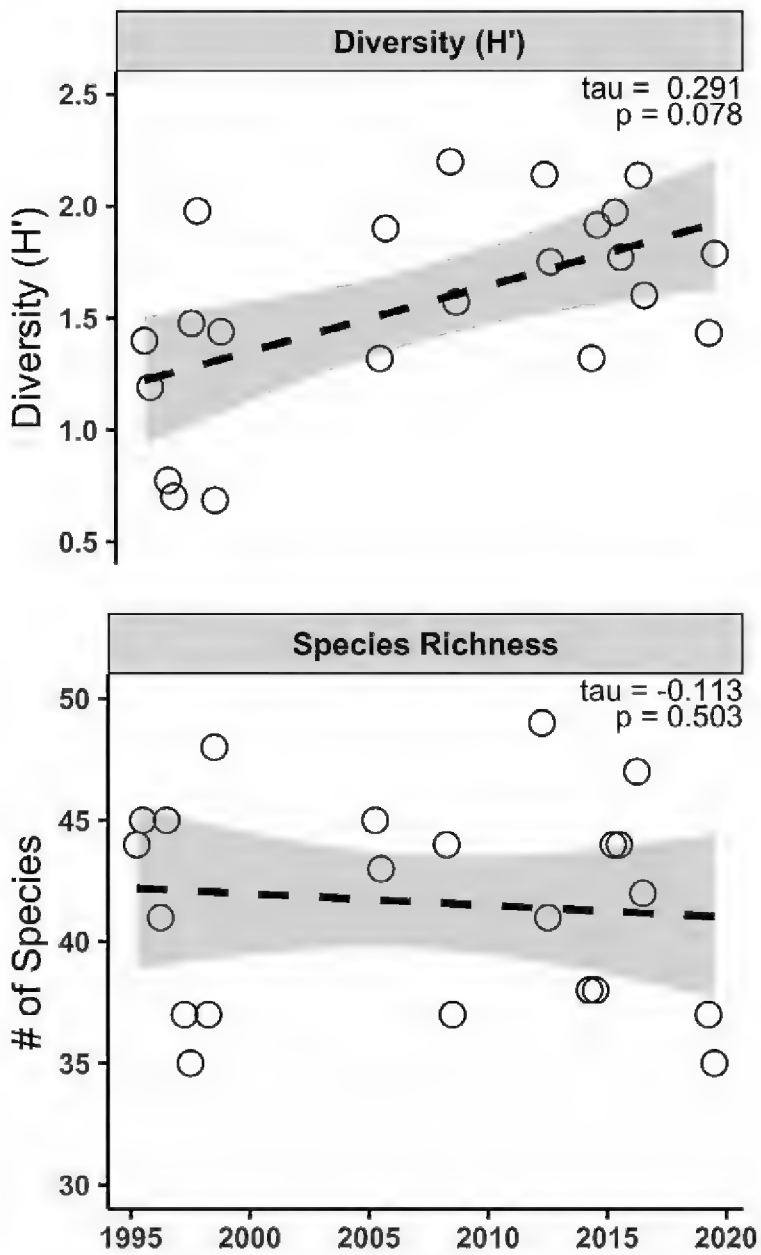

Fig. 7. Shannon H' diversity (top) and species richness (bottom) by sample month over the interrupted time series in San Diego Bay from April 1995 to July 2019. Dashed line and gray shading illustrate the linear regression line and 95% confidence intervals.

the 1970s to the 2000s. Fishes entrapped by the power plants declined by 78% and a 72% decline was reported in the overall abundance of larval fishes in the CalCOFI time series. These trends, which predominantly affected taxa with cool-water affinities, were shared by the fishes of San Diego Bay from 1995 to their series end in 2019. These declines were significantly correlated with declining zooplankton displacement volumes across the California Current System (CCS), which suggests the influence of large-scale climatic and oceanographic drivers.

As Miller and McGowan (2013) and Koslow et al. (2015) both noted, many of the most abundant taxa in the CCS reflects a decline of 72% in the overall abundance of larval fish in the CalCOFI time series between the decades of 1972 to 1981 and 2002 to 2011. Much of this decline was attributed to the decline of northern anchovy and Pacific hake, the two most abundant larval fishes in the CalCOFI data set. However, their reported overall larval fish abundance over this time-period declined 31% even with these two species removed. As northern anchovy ranked as the most abundant species in San Diego Bay, its decline as well as the overall decline in the forage fishes combined probably reflect these similar decreases identified in larval fish abundance in the CCS and the SCB. Overall declines in forage fish species throughout the SCB may have implications for the predators that rely

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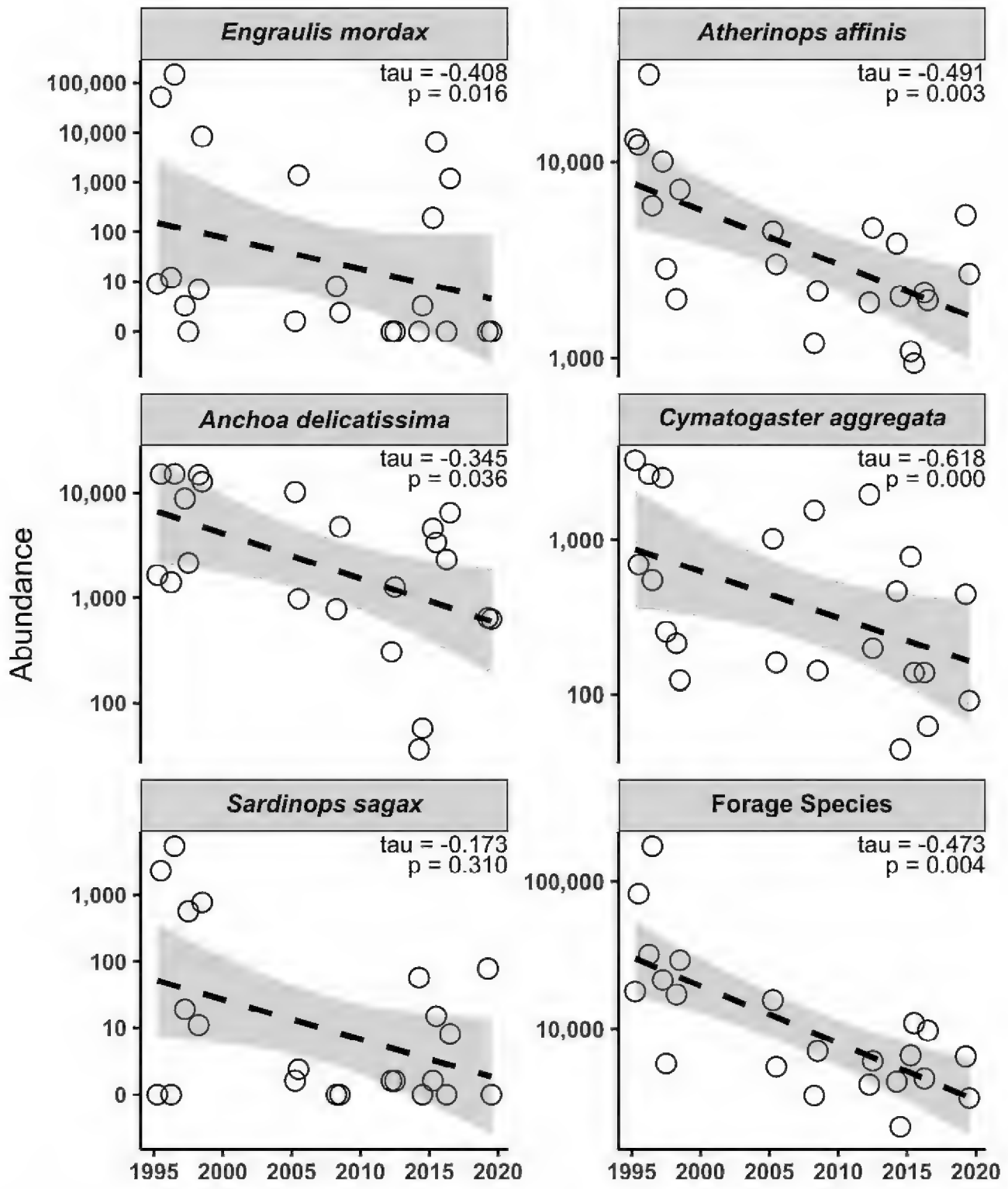

Fig. 8. Time series of the abundance of the top five most abundant species with the five combined as forage species by sample month over the interrupted time series in San Diego Bay from April 1995 to July 2019. Dashed line and gray shading illustrate the linear regression line of log-transformed abundance and 95% confidence intervals.

on these species. Several species of marine mammals, and seabirds have been impacted by declines in prey resources (Sydeman et al. 2015; McClatchie et al. 2016), though these impacts can be offset by other more abundant species if the predator is a generalist and is able to switch between prey species. However, if multiple prey species are in decline, as is the case in San Diego Bay, where four of the top five forage fish species are significantly declining, impacts to the larger food web may be more likely to occur.

The more rarely identified increases in abundance of spotted sand bass and dwarf perch in San Diego Bay from 1995 to 2019 stand in stark contrast to the overall trend of decreasing abundance. The spotted sand bass is at the northern end of its biogeographic ranges in southern California and potentially increased due to the prevailing warmer sea

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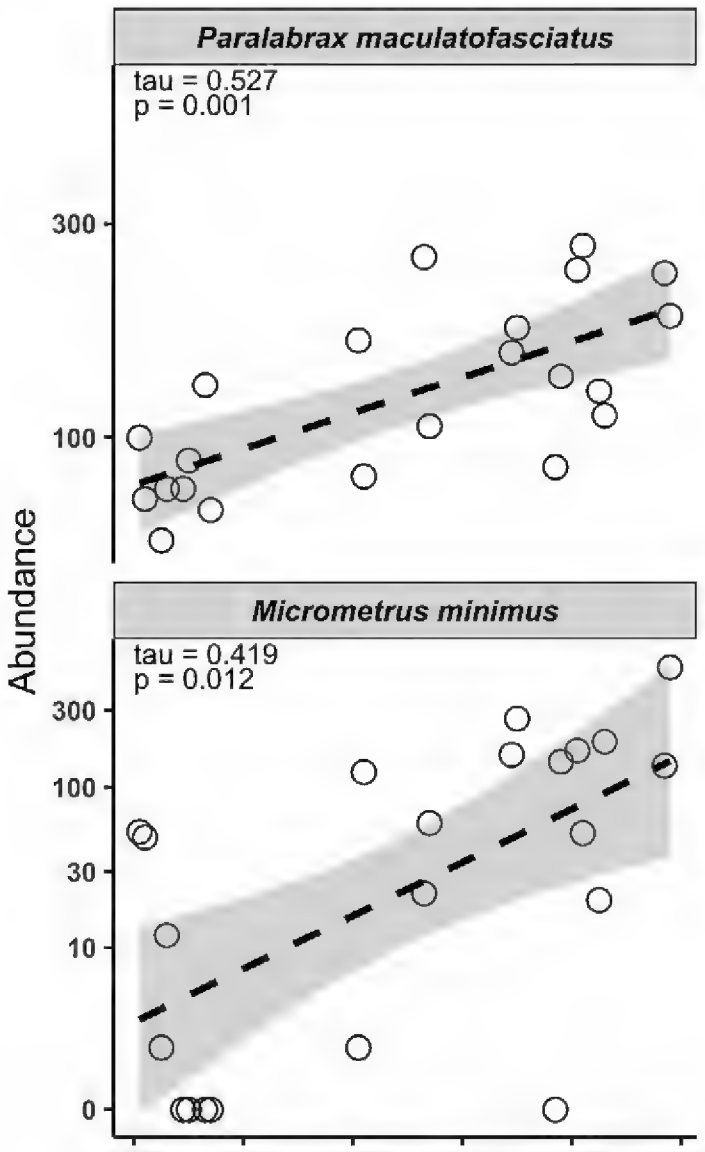

Fig. 9. Abundance of the two species exhibiting increases by sample month over the interrupted time series in San Diego Bay from April 1995 to July 2019. Dashed line and gray shading illustration the linear regression line of log-transformed abundance and 95% confidence intervals.

surface temperatures (SST) since 2010 in the SCB as found in Miller and McGowan (2013). Further, Allen et al. (1995) concluded that spotted sand bass recruitment in the SCB was highest in summers where the SSTs were over 20°C in the SCB as was true in San Diego Bay throughout our study period. Additionally, fisheries management of spotted sand bass changed in 2013 increasing the minimum size to 35.56 cm TL (14"), which was previously 30.48 cm TL (12") and reduced bag limit of 5 (down from 10) (Belquist et al. 2017). Reduction of catch and increased size have the potential to increase the spawning stock and associated biomass of spotted bay bass (Erisman et al. 2011, Jarvis et al. 2014).

The increase in dwarf perch is more complicated and potentially more important with respect to habitat conservation and restoration. Dwarf perch are live-bearers and therefore independent of larval fish abundance indices. Warmer waters may positively impact the nursery ground function of the bay, but likely would not positively effect dwarf perch abundance directly as water temperatures in the bay already approach the dwarf perch's critical thermal maximum (Shrode et al. 1982). Dwarf perch rely on eelgrass beds during many life stages (Schultz 1993) and over the study period eelgrass has increased by approximately 150%. Of note, dwarf perch help control eelgrass-damaging epiphytes and grazers allowing for increased eelgrass growth and production (Lewis and Anderson 2012). With the observed increase in both eelgrass cover and dwarf perch density in San Diego Bay,

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we may be observing *in situ* large-scale positive feedback between a foundational, habitat-forming species and a microcarnivore that lives in that habitat.

The changes in abundance of several San Diego Bay species do not overshadow that the vast majority (71%) of species (25 out of top 35 species) were not found to change significantly over time. Unlike in Morro Bay, where species composition shifted following the loss of 90% of eelgrass habitat (O'Leary et al. 2021), species composition in San Diego Bay remained similar over the study period while eelgrass coverage increased. Furthermore, diversity and species richness did not change significantly over time. We believe stability in species assemblages, composition, and richness over time reflects the resilient nature of the ichthyofauna of San Diego Bay identified by Allen et al. (2002).

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Longevity in Wild California Red-legged Frogs (*Rana draytonii*) from Baja California, México

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Many amphibian species in western North America have been studied to the extent that their general natural history can be broadly defined (Storer 1925; Stebbins 1951, 2003; Grismer 2002). However, one aspect that appears to remain enigmatic in many amphibian species is longevity (i.e., life span) in the wild. Extended longevity of a species can be associated with fitness (Blanco and Sherman 2005), elevation (Liao and Lu 2010) and has also been correlated with brain size (Yu et al. 2018), yet it is a difficult aspect of a species natural history to investigate and determine (Smirina 1994; de Magalhães and Costa 2009). Skeletochronology has been used to determine age of some species of amphibians, with a relatively high level of accuracy (Hemelaar 1981). In other cases, direct observation has been used to age specimens (Conant and Hudson 1949; Engeman and Engeman 1996). Although Smirina (1994) suggested that mark recapture studies are not practical for determining age of individuals in wild populations, new technologies that include small, implanted Passive Integrated Transponders (PIT tags) have simplified this method when associated with long-term studies.

In Mexico, California red-legged frog populations are declining dramatically, mainly due to anthropogenic stresses, including ground water mining, habitat conversion, and spread of exotic species (Peralta-Garcia 2016). We engaged in a long-term and ongoing study of the population dynamics of several California red-legged frog (*Rana draytonii*) populations at several locations of northern Baja California, Mexico. In our study we marked and recaptured individual frogs over years that provided evidence of a maximum life span that exceeds previously reported life spans for the species. Herein, we report on the longevity of wild individuals of the species and speculate on the reasons why the species is long-lived.

Beginning in 2013, while conducting an investigation of California red-legged frogs at the few remaining locations in Baja California where the species is extant, we collected and tagged individual frogs, using 12 mm implanted subdermal PIT tags (www.avidid.com) in anticipation of later recapturing the frogs to determine population patterns at these sites. At two locations, the El Potrero Ranch (30.893575° N, 115.475105° W; elev. approx. 910 m) on the Santo Domingo River, and La Grulla Meadow in the Parque Nacional Sierra San Pedro Mártir (30.914495° N, 115.643678° W; elev. approx. 2060 m), at the headwaters of the Santo Domingo River, we captured all adult and subadult frogs we encountered and marked them for long-term population analysis. Frogs were released unharmed at the site of capture. We assumed the minimum possible age for adults (based on morphology and

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Fig. 1. Adult California red-legged frog (*Rana draytonii*) from La Grulla Meadow, Baja California, Mexico, in 2013, with a minimum age range of 13 yrs upon third capture in 2022. Red arrow indicates insertion point for PIT tag. Photo by B. Hollingsworth.

reproductive status) is that of sexual maturity as stated by Stebbins (1951) and Jennings and Hayes (1994), approximately 2–4 yrs old.

In subsequent years many previously tagged frogs were recaptured during annual visits to the El Potrero site, and also during visits to the La Grulla site, which were visited from 2013 to 2017, 2021 and 2022. Among the many recaptures, three adult frogs marked as adults in 2013, were recaptured in 2020 (one male from El Potrero), 2021 (one female from La Grulla) and 2022 (a second female from La Grulla). This resulted in a known minimum age of 7, 8 and 9 yrs, respectively. If we assume the minimum age at sexual maturity is at least 2–4 yrs, these individuals would have been a minimum age range would be 9–13 yrs old.

A report by Engeman and Engeman (1996) noted that a woodhouse's toad (*Anaxyrus woodhousii*) was known to live 27 yrs in the wild, but this individual was in a semi-natural location—entrapped in a basement window well. Stebbins (1951) reported captive northern red-legged frogs (*R. aurora*) that lived 12–13 yrs, and another approximately 15 yrs, but noted most of the life span of these frogs was in captivity; his account was not attributed, but we found that it was likely that of Cowan (1941). Duellman and Trueb (1994) reported that amphibians tend to be longer lived in captivity than in the wild, which has also been supported by work from others (i.e., Conant and Hudson 1949; Zhang and Lu 2012). We reviewed the maximum age of similar-sized ranid frogs from North America reported in the literature. Similar-sized frogs were reported based on the contention by Duellmann and Trueb (1994) that larger species tend to live longer than smaller species. We found that the average maximum life span among ten similar-sized ranids was 7.7 yrs (Table 1).

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Table 1. Maximum age of reported for wild ranid frogs.

Species	Maximum age	Source
Rana boylii	8	Marlow et al. 2016
R. draytonii	13	This study
R. esculenta	10	Cogalniceanu and Miaud 2003
R. lutriventris	7	Reaser 2000
R. muscosa	10	Matthews and Miaud 2007
R. pipiens	5	LeClair and Castanet 1987
R. sylvatica	5	Bastien and Leclair 1992
Lithobates catesbeianus	9	Shirose and Brook 1995
L. clamitans	6	Shirose and Brook 1995
L. septentrionalis	6	Shirose and Brook 1995
L. subaquavocalis	11	Platz et al. 1997

We speculate that the California red-legged frog is well adapted to a highly variable climate in California and Baja California. Since it reaches sexual maturity several years after metamorphosis, it seems likely that it would be a long-lived species. This may be supported by a need to forgo breeding in unfavorable conditions, particularly recurrent drought-prone areas (J. Alvarez, unpublished data) because a longer-lived species could then survive dry periods and still have opportunities for breeding during subsequent years. Yu et al. (2018) suggested that larger brained frogs may live longer. Several researchers have suggested that anurans living at higher elevations live longer (Lai et al. 2005; Liao and Lu 2010; Oromi et al. 2012). Indeed, this species lives at a wide range of elevations from <1 m in Marin County, California to 2060 m in La Grulla Meadow, Baja California. Our data suggest that longevity occurs at both middle (El Potrero) and high elevations (La Grulla), but we have no data for lower elevations to which to compare.

This age study provides evidence of the minimum lifespan of the California red-legged frog. Future research may provide additional data to support our contention that California red-legged frog evolved to be long-lived. Our data indicate that the three wild frogs reported here likely represent the maximum lifespan currently known for California red-legged frog. Our study is on-going and additional data in future years will likely provide further insights on the longevity of this species.

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Status of Lompoc Yerba Santa *Eriodictyon capitatum* (Namaceae): an Endangered Plant in Santa Barbara County, Southern California

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Abstract.—Lompoc yerba santa *Eriodictyon capitatum* (Namaceae) is an evergreen shrub endemic to west Santa Barbara County in coastal southern Calif. The species was listed as rare under the Calif. Endangered Species Act in 1979 and as endangered under the U.S. Endangered Species Act in 2000. At Federal listing in 2000, Lompoc yerba santa was known from four locations (five occurrences) in three geographic areas. In 2022, the species is known from 11 occurrences in four geographic populations of which 10 occurrences are considered extant and 1 occurrence likely extirpated: Orcutt Oil Field in the Solomon Hills, 2 occurrences; Burton Mesa on Vandenberg Space Force Base North, 6 occurrences; La Salle Canyon on Vandenberg Space Force Base South, 1 occurrence; and Santa Ynez Mountains, 2 occurrences. Lompoc yerba santa occurs mostly in chaparral and bishop pine (*Pinus muricata*) forest, and most occurrences are in sandy soil. The species stands up to 5 m tall and with vertical stems up to 10 cm diameter. Much of its reproduction appears to be vegetative by rhizome production, suggesting low dispersal ability, and it is a habitat specialist with apparent dependence on substrate disturbance and fire. Using all available information and international standards with a precautionary but realistic attitude to uncertainty, Lompoc yerba santa in 2022 meets IUCN criteria for endangered status: the small extent of occurrence is 433 km^2 (<5,000 km^2) and the small area of occupancy is 2.30 km^2 (<10 km^2), along with the geographic range being severely fragmented, and the quality of habitat is observed/inferred/projected to be in continuing decline (altered fire regime/fire management practices, climate change with severe drought and increased temperatures).

Lompoc yerba santa *Eriodictyon capitatum* (Namaceae; Luebert et al. 2016; Fig. 1) is an evergreen shrub endemic to west Santa Barbara County in coastal southern Calif. (Fig. 2). The species was listed as rare under the Calif. Endangered Species Act in 1979 (CDFW 2016), and as endangered under the U.S. Endangered Species Act in 2000 (USFWS 2000). It is recognized also as a 1B.2 rare plant (moderately threatened) by the Calif. Native Plant Society (2021).[1] At Federal listing in 2000, Lompoc yerba santa was

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[1] California Native Plant Society. 2021. Lompoc yerba santa. In Inventory of Rare and Endangered Plants of California. (online edition, v9-01 1.0). Available from: https://www.rareplants.cnps.org. Accessed December 2021.

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Fig. 1. Lompoc yerba santa *Eriodictyon capitatum* (Namaceae) in flower on 24 April 2019 along Cementario Road, on side ridge off Tranquillon Ridge, west end of Santa Ynez Mountains, Hollister Ranch, 490 m elevation, southwest Santa Barbara County, Calif. (occurrence 5). Photo by Heather E. Schneider.

known from four locations in three geographic areas: one location on private land in the Orcutt Oil Field, Solomon Hills, northwest Santa Barbara County; two locations on Vandenberg Space Force Base, west central Santa Barbara County; and one location on private land at the west end of Santa Ynez Mountains, southwest Santa Barbara County. Using 2022 standards (CDFG 2011), these four locations comprised five occurrences: occurrence 1 in the Orcutt Oil Field; occurrences 2, 9, and 10 on Vandenberg Space Force Base North;

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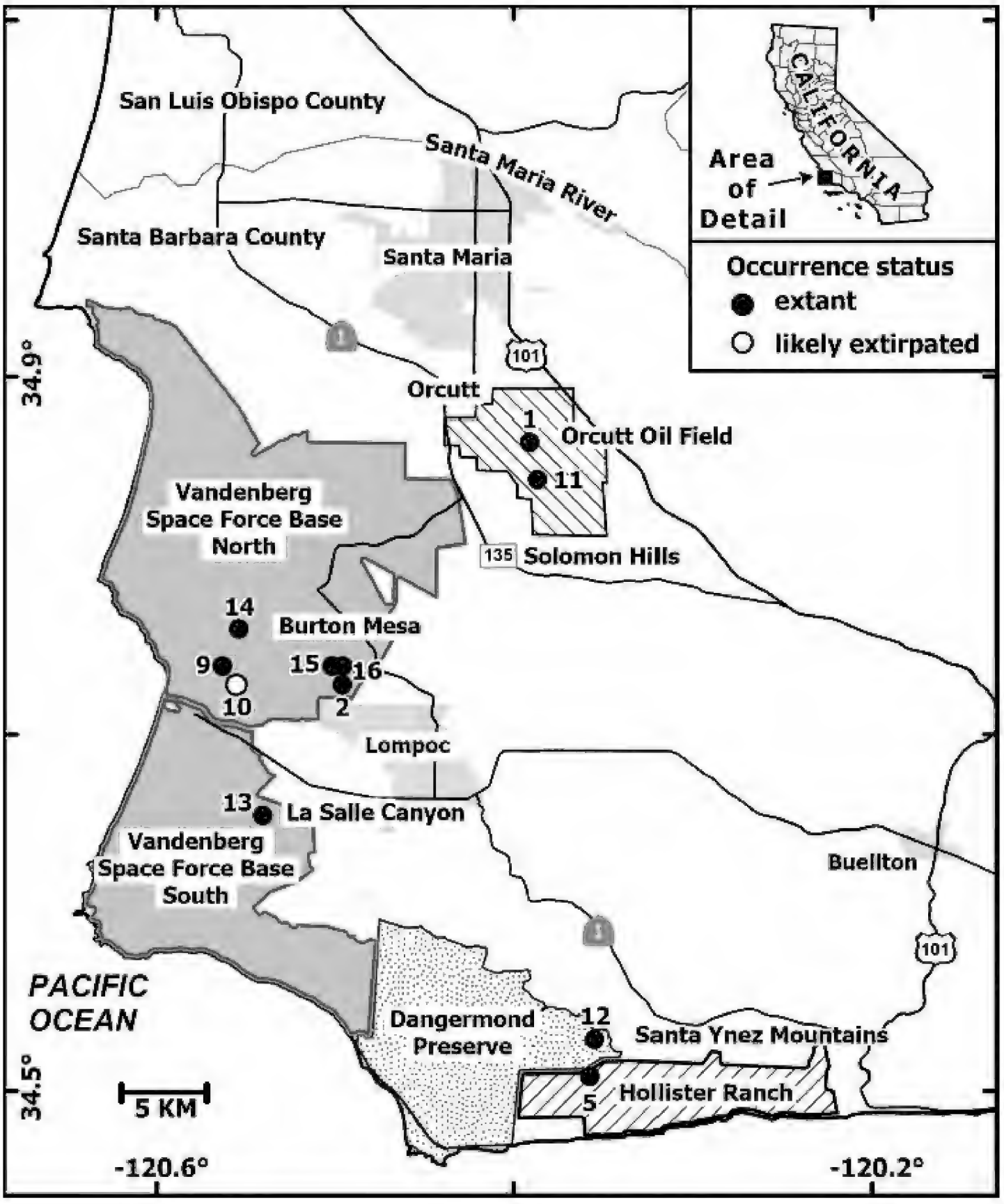

Fig. 2. Geographic distribution of the 11 known occurrences of Lompoc yerba santa *Eriodictyon capitatum* (Namaceae), endemic to west Santa Barbara County, Calif. We recognize four geographic populations, which from north to south are Solomon Hills (occurrences 1 and 11), Burton Mesa (occurrences 2, 9, 10, 14, 15 and 16), LaSalle Canyon (occurrence 13), and Santa Ynez Mountains (occurrences 5 and 12). Adapted from U.S. Fish and Wildlife Service (2021).

and occurrence 5 at west end of the Santa Ynez Mountains. At time of listing, USFWS (2000) identified the following threats: invasive plant species (considered the most severe threat), fire management practices and alteration of natural fire cycles, low seed production and loss of reproductive vigor, small population size (total number of individuals of the species), natural catastrophic events, development, lack of protection (none of the oc-

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currences were protected), habitat fragmentation and alteration of species composition and vegetation structure, limited habitat and extremely limited distribution or reduced distribution resulting from loss of habitat, military activities, facility accidents by oil companies and the military, lack of active management, and lack of a species management plan by the military. The purpose of our paper is to review and enhance the knowledge of Lompoc yerba santa, in particular its distribution, ecology, abundance, threats, management and conservation status in 2022.

Materials and Methods

The region in which Lompoc yerba santa occurs has a Mediterranean climate with mild, wet winters and moderately warm, dry summers, which is strongly influenced by the prevailing westerly oceanic winds. A marine layer of fog advances inland from the Pacific Ocean and is heaviest during late spring and early summer mornings (USFWS 2013). The wet season in this semi-arid region is October to May with high precipitation variability and a long history of multi-year droughts (Oakley et al. 2018). The general geology is comprised of remnants of ancient, uplifted sand dunes now forming a weakly cemented sandstone that weathers to produce a well-drained, sandy and nearly infertile soil. Of particular relevance are the Solomon Hills, Burton Mesa and Santa Ynez Mountains where USFWS (2000) reported Lompoc yerba santa to occur in central coast maritime chaparral and in southern bishop pine forest that intergrades with chaparral.

Little has been published regarding Lompoc yerba santa. In this paper, we use our own data and data provided to us from species experts, along with the sparse published literature, information in the Calif. Natural Diversity Database ([CNDDB] CDFW 2020), unpublished reports, and other documents in files of Vandenberg Space Force Base and USFWS to provide a status review of the species. Using all available information, we summarize the body of knowledge of Lompoc yerba santa, including its distribution, known occurrences, ecology, abundance, threats, management and conservation status in 2022. We considered a location with the species as a separate occurrence if it was >0.4 km from the nearest occurrence (CDFG 2011). International Union for Conservation of Nature [IUCN] (2014) defines extent of occurrence as the area contained within the shortest continuous imaginary boundary that can be drawn to encompass all known locations with the species. IUCN (2014) defines area of occupancy as the area within the extent of occurrence that is occupied by the taxon. Latitude, longitude and elevation were determined with a global positioning system (GPS) device in the field or by using Google Earth aerial imagery and tools. Common and Latin names of plants generally follow Baldwin et al. (2012). Throughout this paper, our use of the word "stem" refers to a vertical vegetative part of Lompoc yerba santa emerging above ground, and such vertical stems may include ramets (genetically identical stems derived from one progenitor) arising from rhizomes (underground shoots that spread horizontally and send up new vertical stems). However, in our analysis of reports by other observers, it was often impossible to determine the intended use of the words "stem," "ramet," "individual" and "plant," and it was often confusing and inconsistent from one observer to the next. Therefore, we repeat the numbers of the structures precisely as reported by the particular observer, and in Table 1 we provide the reported numbers in the 11 known occurrences. The stated numbers should be considered best approximations due to the non-uniform counting methods of various persons and the sometimes-difficult landscapes in which the plants occur. Likewise, the stated distances and areas should be considered best approximations. In Table 2 we summarize the conserva-

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Table 1. Reported numbers of Lompoc yerba santa *Eriodictyon capitatum* in the 11 known occurrences, Santa Barbara County, Calif. Adapted from U.S. Fish and Wildlife Service (2021) where sources of data are referenced.

	Occurrence										
Year	1	2	5	9	10	11	12	13	14	15	16
2022		observed					12 stems				
2021					not found						
2019		unknown number	observed	743 stems 316 ramets	not found				70 individuals 78 ramets		unknown number
2018	>7,000 ramets			804 stems 617 ramets				281 stems 258 ramets			
2017				627 stems 507 ramets							
2016		>200 plants in part		651 stems 616 ramets							
2015	500-1,000 individuals	9,794 stems in part		958 stems 733 ramets	not found	unknown number				5 stems 4 ramets	28 ramets
2014							2 individuals				
2013	common, 100's of individuals	150 individuals in part		250+ ramets			2 individuals				
2012		150 individuals in part		80 individuals			5 individuals				
2011		200 ramets in part		80 ramets		100-135 individual plants					
2010		665 ramets in part		807 ramets							48 ramets
2007						20-30 individuals					
2006		645 ramets in part		1,017 ramets	not found						20 ramets
2005					not found						

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Table 1. Continued

	Occurrence										
Year	1	2	5	9	10	11	12	13	14	15	16
1995		>100 stems in part		>100 stems							
1993	common	63 ramets in part		>100 ramets							
1992		observed									
1987		8 individuals in part		<500 individuals?	several shrubs						
1986	>500 individuals		100+ stems	locally common							
1983				56 clumps in part							
1982		68 stems in part		>100 stems							
1973	common										
1960			common								
1957			common								
1932		observed									

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Table 2. Conservation status of the 11 known occurrences of Lompoc yerba santa *Eriodictyon capitatum*, Santa Barbara County, Calif. Occurrences 12, 13, 14, 15 and 16 are new. Climate change = climate change with severe drought and increased temperatures. Adapted from U.S. Fish and Wildlife Service (2021).

Occurrence	Location	Landowner	Protected	Managed	Year last observed	Status in 2022	Threats in 2022
1	Orcutt Oil Field in Solomon Hills	Pacific Coast Energy Company	N	N	>7,000 ramets in 2018	presumed extant	development, oil production and spills, dense vegetation, lack of management, road vehicles running over plants, road maintenance, altered fire regime/fire management practices, climate change
2	Vandenberg Space Force Base (north base)	U.S. Space Force	N	Y	unknown number in 2022, 9,794 stems in part in 2015	extant	military activities, development, dense vegetation, low seed production, erosion, altered fire regime/fire management practices, climate change
5	Hollister Ranch	multiple private	N	N	observed in 2019, 100+ stems in 1986	presumed extant	development, dense vegetation, lack of management, road vehicles running over plants, road maintenance, altered fire regime/fire management practices, climate change
9	Vandenberg Space Force Base (north base)	U.S. Space Force	N	Y	743 stems/316 ramets in 2019	presumed extant	military activities, development, road maintenance, low seed production, invasive species, altered fire regime/fire management practices, climate change
10	Vandenberg Space Force Base (north base)	U.S. Space Force	N	Y	several shrubs in 1987, not found in 2021	likely extirpated	military activities, development, small number of plants, invasive species, altered fire regime/fire management practices, climate change
11	Orcutt Oil Field in Solomon Hills	Santa Maria Energy	N	N	unknown number in 2015, 100-135 individual plants in 2011	presumed extant	development, oil production and spills, dense vegetation, lack of management, road vehicles running over plants, road maintenance, altered fire regime/fire management practices, climate change
12	Jack and Laura Dangermond Preserve	The Nature Conservancy	Y	N	12 stems in 2022, 5 individuals in 2012	extant	small number of plants, presumed low genetic diversity, potentially uniclonalism, dense vegetation, lack of management, altered fire regime/fire management practices, climate change
13	Vandenberg Space Force Base (south base)	U.S. Space Force	N	Y	281 stems/258 ramets in 2018	presumed extant	military activities, low genetic diversity, altered fire regime/fire management practices, climate change
14	Vandenberg Space Force Base (north base)	U.S. Space Force	N	Y	70 individuals/78 ramets in 2019	presumed extant	military activities, development, small number of plants, dense vegetation, altered fire regime/fire management practices, climate change
15	Vandenberg Space Force Base (north base)	U.S. Space Force	N	Y	5 stems/4 ramets in 2015	presumed extant	military activities, small number of plants, dense vegetation, altered fire regime/fire management practices, climate change
16	Vandenberg Space Force Base (north base)	U.S. Space Force	N	Y	unknown number in 2019, 28 ramets in 2015	presumed extant	military activities, development, small number of plants, dense vegetation, altered fire regime/fire management practices, climate change

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tion status of each occurrence of Lompoc yerba santa in 2022, including the threats. In Appendix 1 we discuss each occurrence according to its assigned number in the CNDDB (CDFW 2020), which range between 1 and 16 because five previously recognized occurrences were combined with others as knowledge of distribution increased. This present paper emanates mostly from unpublished USFWS (2021), for which two of us are the primary authors and to which the other four contributed substantially. In addition, two of us (CMG, KEH-L) provide genetics information as currently known in a separate study underway on population genetics of Lompoc yerba santa. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of USFWS or U.S. Space Force.

Results and Discussion

Biology and Ecology.—Lompoc yerba santa is one of 11 species (plus additional subspecies and varieties) in the genus *Eriodictyon* that occurs in southwest United States and north Baja Calif., Mexico (Maher et al. 2020).[2] Eastwood (1933) described Lompoc yerba santa based on the holotype specimen CAS194986 collected in 1932 by Ralph Hoffman, "five miles north of Lompoc on the road to Casmalia, Santa Barbara County, Calif., growing under *Pinus muricata* [bishop pine]." Plants are reported to stand up to 5 m tall and with stems up to 10 cm diameter (Oyler et al. 1995). It is a woody evergreen shrub with shredding bark and narrow, linear leaves (4 to 9 cm long, 0.2 to 0.5 cm wide; Fig. 1) that are sessile (leaf blade attached directly to branch) on sticky branches with the leaf margin strongly rolled under. The flowers have funnel-shaped, lavender corollas (6 to 15 mm long) and are clustered in head-like inflorescences (2.5 cm wide) at the tips of branches, blooming from April to July. The fruits are capsules with four valves. Lompoc yerba santa is distinguished from all other species of *Eriodictyon* by combination of its linear leaves and head-like inflorescences.[2]

Lompoc yerba santa is considered an early successional, pioneer and edge species, exhibiting opportunistic resprouting by ramets, sometimes in response to disturbance (Schneider et al. 2021). The species is known to grow along roads and trails, on exposed ridge tops, on slopes and in a canyon bottom, in open areas, and at edge of and within dense vegetation. It occurs mostly in chaparral and bishop pine forest, and also in sage scrub and oak woodland. Most occurrences of Lompoc yerba santa are in sandy soil, and parts of two occurrences (1 and 2) are in shale. The primary constituent elements for its designated critical habitat are: sandy, acidic soil; and maritime chaparral, and bishop pine forests that intergrade with chaparral (USFWS 2002). These are the physical and biological features essential to conservation of Lompoc yerba santa and may require special management considerations. Common associated species include bishop pine, black sage *Salvia mellifera*, Calif. sagebrush *Artemisia californica*, ceanothus *Ceanothus* sp., chamise *Adenostoma fasciculatum*, coast live oak *Quercus agrifolia*, coyote brush *Baccharis pilularis*, and La Purisima manzanita *Arctostaphylos purissima*. In particular, the latter species occurs in most locations with Lompoc yerba santa on Vandenberg Space Force Base and in all nearby suitable habitat.

Lompoc yerba santa reproduces both sexually by seeds and asexually by rhizomes. The species is self-incompatible, meaning pollen from another genetically-distinct individual

[2] Hannan, G.L. 2021. *Eriodictyon*. In Jepson Flora Project (eds.), Jepson eFlora, Revision 9. Available from: https://ucjeps.berkeley.edu/eflora/eflora_display.php?tid=9648. Accessed February 2022.

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is required for fertilization of flowers. Experimentally self-pollinated flowers produced a mean of 0.03 seed per fruit (Elam 1994), whereas experimentally cross-pollinated flowers produced a mean of 1.77 seeds per fruit. The following floral visitors to Lompoc yerba santa have been observed (Knapp 2013b; Schneider et al. 2021; our data): bee fly (Bombyliidae), carpenter ant *Camponotus* sp., small carpenter bee *Ceratina* sp., sweat bee *Agapostemon* sp., sweat bee *Halictus* sp., incomplete sweat bee *Lasioglossum incompletum*, honey bee *Apis* sp., bumblebee *Bombus* sp., yellow-faced bumblebee *Bombus vosnesenskii*, leaf beetle (Chrysomelidae), tumbling flower beetle (Mordellidae), soft-wing flower beetle (Melyridae), and northern checkspot butterfly *Chlosyne palla*. The species can spread vegetatively by rhizomes, thus producing colonies of ramets from only one or a few genetically-distinct individuals (Elam 1994). Several of the 10 extant occurrences comprise only one to a few colonies, suggesting low genetic diversity for the species.

Roof (1988) commented that seedlings of *Eriodictyon* species are not often observed in the wild. After experimentation, he speculated that most seeds of *Eriodictyon* species do not germinate and that most seedlings do not survive in the wild. He stated that in most experimental attempts to germinate seeds of *Eriodictyon* species, no seedlings were obtained. Of the eight species he tested, Lompoc yerba santa was the only one with tolerance to shade, whereas seedlings of the other species were easily killed by shading. Two species of *Eriodictyon* (hairy yerba santa *E. trichocalyx*, thickleaf yerba santa *E. crassifolium*) are known to be facultative seeders and resprouters in their fire-prone ecosystems (Keeley et al. 2006). Seed germination of Lompoc yerba santa is stimulated by smoke, with seeds germinating faster and at higher rates when treated with liquid smoke and in darkness when compared with other treatments and a control (Schneider et al. 2021). In some other species of *Eriodictyon*, germination is triggered by combinations of heat shock from fire, smoke, and exposure to charate (wood with leachable chemicals known to stimulate germination; Keeley and Nitzberg 1984; Keeley 1987, 1991; Keeley et al. 2005; Gamboa-deBuen and Orozco-Segovia 2008). Schneider et al. (2021) suggested that Lompoc yerba santa is adapted to fire, and that fire could promote genetic diversity within an occurrence by stimulating a flush of germination from the soil seed bank. Occurrences 9, 16 and part of 13 appear to be the only occurrences to have burned in the past 150 yr.[3]

Distribution and Abundance.—In 2022, we recognize 11 occurrences of Lompoc yerba santa: 1, 2, 5, 9, 10, 11, 12, 13, 14, 15 and 16. We presume 10 of these occurrences to be extant in 2022 by recent visitation, and one occurrence to be likely extirpated (occurrence 10). Five of these occurrences are new (occurrences 12, 13, 14, 15 and 16) since USFWS (2011) reviewed the status of Lompoc yerba santa in 2011 and recognized six occurrences (occurrences 1, 2, 5, 9, 10 and 11). Specifically, occurrence 12 became recorded in the CNDDB in 2019, and occurrences 13, 14, 15 and 16 became recorded in 2021 as a result of our analyses. We recognize four geographic populations based on landscape features and distance, which from north to south are the following (Fig. 2): Solomon Hills (occurrences 1 and 11), Burton Mesa (occurrences 2, 9, 10, 14, 15 and 16), La Salle Canyon (occurrence 13), and Santa Ynez Mountains (occurrences 5 and 12).

The Solomon Hills geographic population (190 to 390 m elevation) is 1.7 to 3.1 km south of Orcutt and 18.0 to 19.7 km inland east from the Pacific Ocean. It comprises occurrences 1 and 11 in west Santa Barbara County, with occurrence 1 being northmost for the species.

[3] SB Atlas Admin. 2021. Fire portal and regional priority planning project. Available from: https://databasin.org/articles/52a6d858c8914d758e6bef95111ca482/. Accessed June 2021.

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Both occurrences are in the Orcutt Oil Field on private properties owned/leased by Pacific Coast Energy Company and Santa Maria Energy, respectively, and the properties are used for oil and gas production. More than 7,000 ramets were recorded at occurrence 1 in 2018 (Santa Barbara Botanic Garden 2019; Table 1), making occurrence 1 the largest or second largest occurrence for the species and with high genetic diversity (our data), whereas occurrence 11 is small with 100 to 135 individual plants recorded in 2011.[4] Identified threats at both occurrences in 2022 are development, oil production and spills, dense vegetation (includes competitive native species), lack of management, road vehicles running over plants, road maintenance, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

The Burton Mesa geographic population (43 to 126 m elevation) is 2.6 to 8.9 km inland east from the Pacific Ocean. It comprises occurrences 2, 9, 10, 14, 15 and 16, all on north base (north of West Ocean Avenue near Santa Ynez River) of Vandenberg Space Force Base in west Santa Barbara County. Lompoc yerba santa is included in the installation's Integrated Natural Resources Management Plan (USAF 2014), which is a military planning document with strategies and programs to protect biological resources on the base where not in direct conflict with the operational mission. From 2006 to 2022, management efforts for the species included census surveys at known locations, searches for new locations, removing invasive species in occupied and nearby habitat (441 ha/1,090 ac treated), one outplanting project (not successful), and facilitating genetics research. In 2015, 9,794 stems were recorded in part of occurrence 2 (our data), making it the largest or second largest occurrence for the species and with high genetic diversity (our data). Lompoc yerba santa was recorded at occurrence 10 only in 1987 (several shrubs; Griffiths et al. 1987a, b), and it now seems likely extirpated. Searches in 2005, 2006, 2015, 2019 and 2021 did not find any plants. Occurrence 9 (low to moderate genetic diversity, our data) is in an area likely desirable for future development. It had 743 stems/316 ramets in 2019[5] (and our data), which is a decline since 2006 when 1,017 ramets were observed.[5,6] Occurrence 14 (low to moderate genetic diversity, our data) was first identified in 2019 (70 individuals/78 ramets;[5] our data) in the plan area for the MQ-9 Wing Beddown project (USFWS 2020, 2021), but that project will now occur in Florida instead. Occurrence 15 had 5 stems/4 ramets in 2015 (our data), and occurrence 16 had 28 ramets in 2015.[7] Identified threats at all six occurrences in 2022 include military activities, development, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

The La Salle Canyon geographic population (220 to 233 m elevation) is 7.3 km inland east of the Pacific Ocean, and 6.0 km west of Lompoc. It comprises only occurrence 13, in upper La Salle Canyon on south base (south of West Ocean Avenue near Santa Ynez River) of Vandenberg Space Force Base in west Santa Barbara County. There are two

[4] AECOM. 2011. Careaga Oil Field expansion section 7 consultation initiation package. Santa Maria, Calif., 121 pp.

[5] ManTech SRS Technologies. 2020. Threatened and endangered plant surveys on Vandenberg Air Force Base, California, 2019 final report. Lompoc, Calif., 55 pp.

[6] KFS and ManTech SRS Technologies. 2020. Biological assessment for the Ground Based Strategic Deterrent Test Program at Vandenberg Air Force Base, California. Huntsville, Ala., and Lompoc, Calif., 48 pp.

[7] ManTech SRS Technologies. 2015. 2014-2015 Special status plant surveys on Vandenberg Air Force Base, California. Lompoc, Calif., 22 pp.

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colonies, with a total count of 281 stems/258 ramets in 2018 (our data) and low genetic diversity (our data). Identified threats in 2022 are military activities, low genetic diversity, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures. A monoculture of native deerweed *Acmispon glaber* was a threat post-fire to any resprouts and seedlings in the Canyon Fire burn scar in 2019.[5]

The Santa Ynez Mountains geographic population (355 to 533 m elevation) is south of Jalama Creek, 3.7 to 6.3 km inland north of the Pacific Ocean, and 3.4 km southwest of State Highway 1. It comprises occurrences 5 and 12 at west end of the Santa Ynez Mountains in southwest Santa Barbara County. Both occurrences are on private properties. Occurrence 5 is on Hollister Ranch with multiple landowners, and occurrence 12 is on Jack and Laura Dangermond Preserve owned by The Nature Conservancy. The two occurrences are separated by a 2.1 km distance. Occurrence 12 (presumed low genetic diversity, potentially uniclonalism) is small with 12 stems in 2022 (our data). Occurrence 5 (moderate to high genetic diversity, our data) is larger with 100+ stems in habitat rated excellent quality in 1986 (Myers 1987). Identified threats at both occurrences in 2022 are dense vegetation, lack of management, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures; and also at occurrence 5, road vehicles running over plants and road maintenance.

Threats.—Lompoc yerba santa is a habitat specialist with a small geographic range (extent of occurrence 433 km^2), a small area of occupancy (2.30 km^2), and a relatively small, total population (genetically distinct individuals) for the species. The combination of the following life history traits makes it a species that should be considered highly vulnerable to climate change (Anacker et al. 2013): much of its reproduction appears to be vegetative by rhizome production, suggesting low dispersal ability; and it is a habitat specialist with apparent dependence on substrate disturbance and fire. In 2022, Lompoc yerba santa is known from 11 occurrences in four geographic populations in west Santa Barbara County, of which 10 occurrences are considered extant and one likely extirpated. We identify the following threats at one or more occurrences in 2022 (Table 2): military activities, development, dense vegetation (includes competitive native species), lack of management, oil production and spills, invasive species, low seed production, potentially uniclonalism, low genetic diversity, small number of plants, road vehicles running over plants, road maintenance, erosion, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures. Adverse stochastic events are also a threat. All threats identified at time of listing in 2000 were considered ongoing threats in 2011 (USFWS 2011). Development on Hollister Ranch was considered a new threat in 2011, while oil extraction and energy development activities were specifically not considered threats. All threats identified at time of listing and in 2011 (USFWS 2011) are ongoing in 2022, including lack of protection (only occurrence 12 on Jack and Laura Dangermond Preserve is protected). However, seven of the 11 known occurrences are managed in 2022 (none at time of listing), all on Vandenberg Space Force Base that now has a management plan for the species (USAF 2014).

Conclusions

Using all available information and international standards with a precautionary but realistic attitude to uncertainty, Lompoc yerba santa in 2022 meets IUCN (2012, 2014) criteria for endangered status. That is, the taxon is considered to be facing a very high risk of extinction in the wild. This is based upon the following: the small extent of occurrence

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is 433 km^2 (<5,000 km^2) and the small area of occupancy is 2.30 km^2 (<10 km^2), along with the geographic range being severely fragmented (much of its reproduction appears to be vegetative by rhizome production, suggesting low dispersal ability), and the quality of habitat is observed/inferred/projected to be in continuing decline (altered fire regime/fire management practices, climate change with severe drought and increased temperatures).

Coordinated research and conservation are needed to better understand Lompoc yerba santa, and to restore and maintain the 11 known occurrences. We make the following recommendations. (1) In our analysis of reports by other observers, it was often impossible to determine the intended use of the words "stem," "ramet," "individual" and "plant," and it was often confusing and not consistent from one observer to the next. In accordance with international guidelines for colonial and modular organisms (IUCN 2014), we recommend counting the number of all vertical stems and reporting that number as vertical stems (irrespective of genetic distinctiveness) along with a statement of using this particular method. (2) Implement management actions to reduce threats and to benefit the occurrences of Lompoc yerba santa. As a matter of urgency, The Nature Conservancy should make special efforts to manage and enhance occurrence 12 (Jack and Laura Dangermond Preserve) to prevent its extirpation. (3) Conserve and protect habitat in the vicinity of and near existing occurrences, with particular attention to maritime chaparral on Burton Mesa, Vandenberg Space Force Base North. (4) Conduct searches for additional locations of Lompoc yerba santa, including use of helicopters and drones for searching large expanses of potential habitat, especially in difficult terrain. Priority should be given to searching in the following areas: vicinities of occurrence 12 and occurrence 13 (Upper LaSalle Canyon, Vandenberg Space Force Base South), and the area between; and the area between occurrence 14 (Airfield, Vandenberg Space Force Base North) and occurrences 1 and 2 (Orcutt Oil Field, Solomon Hills). (5) Continue seed collection for conservation seed banking. Contingent upon results of previous genetic sampling, multiclonal and potentially multiclonal locations should be visited to determine if seed production is occurring, in particular at occurrences 2 and 11. (6) Collect and cultivate seeds and cuttings to develop protocols for propagation and outplanting for long-term restoration success. In consideration of the threat of climate change with severe drought and increased temperatures, the methods employed for outplanting in arid lands by Abella et al. (2012, 2015, 2020) and Abella (2017) should be considered. (7) Study genetic diversity and reproductive biology, pollinator network and its potential disruption, potential barriers to recruitment, and the species' relationship with fire. (8) Introduce Lompoc yerba santa (with representative genetic diversity) into living collections at several botanic gardens.

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Appendix 1

The 11 known occurrences of Lompoc yerba santa in four geographic populations, Santa Barbara County, Calif.

Solomon Hills Geographic Population

Occurrence 1 (includes previous occurrence 4).—Graciosa Ridge and several adjacent ridges at Newlove Hill in Orcutt Oil Field, Solomon Hills; 34.833663, -120.406974; extent of occurrence 2.19 km^2, area of occupancy <1.73 km^2, 287 to 390 m elevation. The occurrence is 1.7 km south of Orcutt and 2.0 km west of Highway 101 (a freeway), and it is the northmost occurrence of Lompoc yerba santa. It is on three parcels of private property owned/leased by Pacific Coast Energy Company, mostly APN 101-020-074, and also APN 101-020-043 and APN 101-020-041. Mooney (1986a) surveyed and mapped the occurrence in 1986, reporting it on Careaga sandstone and Paso Robles formation (sandstone and shale; Arnold and Anderson 1907). She reported >500 individuals (Table 1) with the plants "scattered to abundant" along ridgetop roads, some growing over old surface pipelines and small structures. The species appeared to prefer little to no developed soil, and with the "healthiest" plants under bishop pine. Sage Institute (2014) reported Lompoc yerba santa and La Purisima manzanita as the two dominant species in the central maritime chaparral at occurrence 1 in 2013, each providing 30% of absolute cover in a rough broken landscape of sandy soil up to 12 inches deep with a restrictive layer of tar beneath. Lompoc yerba santa was prevalent, growing also in disturbed/ruderal areas where it was common, and in mixed bishop pine stands and coast live oak woodlands. Sage Institute (2014) provided a map of the occurrence. Knapp (2013b) reported hundreds of individuals in 2013, some very large along with many young plants. Knapp (2015) observed the species as locally common with 500 to 1,000 individuals, and 90% of these with fruit in late September. Most recently, Santa Barbara Botanic Garden (2019) reported >7,000 ramets in 2018, and our data show high genetic diversity. We observed high seed production in 2018, and likewise D. Knapp (Santa Barbara Botanic Garden, pers. comm. 2022) in 2015. The species was recorded as common on the slopes of Graciosa Ridge with bishop pine in 1973 (label for herbarium specimen UC1426031). Several records in CDFW (2020) report the following: shrub to 2 m tall in a cleared staging area; along roads and in openings in tar sand roads; near and at oil pump pads; in formerly disturbed places in the oil field; and up to 4 m tall. Santa Barbara Botanic Garden (2019) identified excessive disturbance and habitat loss as threats, including roads, oil production and spills, and Knapp (2015) identified fire suppression as a possible threat. We identify the following threats here in 2022 (Table 2): development, oil production and spills, dense vegetation, lack of management, road vehicles running over plants, road maintenance, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

Occurrence 11.—South edge of Orcutt Oil Field (Careaga Lease), Solomon Hills; 34.812419, -120.403018; extent of occurrence 3.2 ha, area of occupancy 0.92 ha, 190 to 206 m elevation; APN 101-020-074. It is 4.3 km south of Orcutt and 4.7 km west of Highway 101. AECOM[4] recorded 100 to 135 individual plants in 2011 and showed three separate groups in their fig. 2: 11A (our designation; area of occupancy 0.40 ha) centered at 34.812101, -120.403082; 11B (area of occupancy 376 m^2) centered at 34.811709, -120.402995 with "50 to 70 individual plants;" and 11C (area of occupancy 0.48 ha) centered at 34.812313, -120.399577 with "a few individuals." However, the stated distances and compass directions appear erroneous because they do not coincide with their fig. 2. Using Google Earth aerial imagery (dated 27 July 2016) and tools, this occurrence is 70 to 450 m south and southeast of intense industrial activity. The three areas of occupancy are on sandy soil (W. Vogler, pers. comm. 2021) and mostly intact with scrub and chaparral on private property owned/leased by Santa Maria Energy. Vogler and Boinay (2007) first observed 20 to 30 "individuals" at 11A in July 2007 with "80% flowering" in coastal sage scrub and chaparral dominated by coyote brush, chamise and black sage. This group is between the private, primary access road to the active oil field and

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an incised ephemeral creek. The slope between the road and creek bank is moderately steep in the western part and gently sloping in the eastern part. Shortly after discovery, Santa Maria Energy placed signs roadside alerting to a restricted area with sensitive habitat and Lompoc yerba santa, and also placed barriers at strategic locations to prevent vehicles leaving the road. Branches of Lompoc yerba santa were extending over the road, and a few stems were growing up through cracks in the asphalt. This group is situated south of the road, and a search was conducted north of it but no plants were seen (Vogler, pers. comm. 2021). Using Google Earth aerial imagery (dated 27 July 2016) and our stated coordinates, we observed this group at the base of a hill and above the upper reaches of a dry creek bed, 67 m south of several industrial buildings, 249 m east of row crops, and 88 m west of a pipe storage facility (plants extend to 30 m of the concrete pads; Vogler, pers. comm. 2021). AECOM[4] reported this elongate area with 50 to 60 "individual plants." 11B is immediately south of 11A and across the creek channel, and AECOM[4] reported this circular area with "a few individuals." 11C is 198 m west of 11A, and it is on hilly land on north side of the upper reach of the same ephemeral creek. A metal guard rail and fencing separate it from most of the intense industrial activity. AECOM[4] reported this elongate area with 50 to 70 "individuals." This occurrence was last observed in 2015 (Vogler, pers. comm. 2021). We identify the following threats here in 2022: development, oil production and spills, dense vegetation, lack of management, road vehicles running over plants, road maintenance, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

Burton Mesa Geographic Population

Occurrence 2 (includes previous occurrence 3).—Santa Lucia Canyon and Lower Pine Canyon (and area between), Vandenberg Space Force Base (north base); 34.702655, -120.507479 center of occurrence; extent of occurrence 32 ha, area of occupancy 6.09 ha, 43 to 112 m elevation. This occurrence comprises eight groups that we refer to as 2A, 2B, 2C, 2D, 2E, 2F, 2G and 2H. Details for the groups are provided below. Threats here include military activities, development, dense vegetation (some locations), low seed production (some locations; Elam [1994] reported high seed production at previous occurrence 3), erosion (bottom of Pine Canyon), altered fire regime/fire management practices, and climate change with severe drought and increased temperatures. Vandenberg Space Force Base is targeting non-native, invasive plants for removal in and near all locations with Lompoc yerba santa. We assign the multiple herbarium specimens with collecting location as "5 miles north of Lompoc on road to Casmalia" to this occurrence. Elam (1994) reported high seed production and multiclonal, high genetic diversity at some locations. Likewise, our data show high genetic diversity for occurrence 2.

2A Lompoc Gate, Santa Lucia Canyon Stand #1 (occurrence 2 in 1983 and 1994): West side of Santa Lucia Canyon near Lompoc Gate (also known as Pine Canyon Gate); 34.706328, -120.504170 (our data); area of occupancy 195 m^2, 75 to 81 m elevation. Smith (1983) observed 27 stems of Lompoc yerba santa under bishop pine in chaparral dominated by manzanita on a steep slope with shale in Santa Lucia Canyon, 307 m northwest of the intersection of Washington Avenue and Santa Lucia Canyon Road. Vegetation cover was thin with large areas of bare ground, which is where he observed most plants. Smith (1983) marked his general location on a map (34.706206, -120.504435; our determination). He presumed this to be the type locality because in 1983 it was the only known location with Lompoc yerba santa: "five miles north of Lompoc on the road to Casmalia …growing under *Pinus muricata*" (Eastwood 1933). However, since then, the species has been identified nearby at 2G, which likewise meets the description for type locality and could just as well be it.[8] Smith (1983) observed many stems connected by rhizomes and a lack of seeds, hypothesizing the colony was uniclonal. Elam (1994) reported the 18 stems/ramets here with few seeds in 1993 to be uniclonal. We observed some plants with her metal tags in 2006. The following numbers have been recorded at group 2A: 1987, 27 stems; 1993, 18 ramets; 2006, 11 ramets; 2010, 5 ramets; 2015, 3 stems/3 ramets (plus several dead); and 2019, 0 plants. The largest recorded "area" is 121 m^2 in 2006 and 2015, and with high quality habitat in 2015[7] (and our data). ManTech[7] identified small number of plants and drought as primary threats at this location in 2015. The counts have declined steadily since 1983 (Smith 1983), and the species may now be extirpated here.

2B Santa Lucia Canyon Stand #2: Upper west slope of Santa Lucia Canyon; 34.704452, -120.505808; area of occupancy 1.1 ha, 80 to 112 m elevation. The Lompoc yerba santa are situated sparsely in gaps

[8] Riecker, P. 1889. Map of the County of Santa Barbara. Riecker, Huber and Mench: San Francisco. Available from: https://www.loc.gov/resource/g4363s.la000038/?r=0.161,0.403,0.742,0.384,0. Accessed July 2021.

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among a dense canopy of Burton Mesa chaparral,[7] dominated by La Purisima manzanita with bishop pine and coast live oak. ManTech[7] observed new growth of ramets in the understory of chaparral die-back in 2015 due to drought, leading them to remark that Lompoc yerba santa appeared to fair well under drought conditions relative to other chaparral species such as La Purisima manzanita. However, they speculated that colonies on dry open slopes are likely susceptible to decline over time while colonies occurring within a dense matrix of other chaparral species may benefit. This location was identified in 2015 by helicopter surveys for Lompoc yerba santa in potential habitat, with confirmation of 56 ramets in at least 10 colonies by ground visitation.[7]

2C Santa Lucia Canyon Stand #3: Floor of side canyon off Santa Lucia Canyon (west side); 34.702522, -120.505976; area of occupancy 0.11 ha, 47 to 60 m elevation. The plants are in an open area surrounded by dense coast live oak. This location was identified in 2015 by helicopter surveys for Lompoc yerba santa in potential habitat, with confirmation of 134 ramets by ground visitation.[7]

2D Pine Canyon Rim Stand: An area spanning across a ridge onto the upper east slope of Pine Canyon and upper west slope of Santa Lucia Canyon; 34.701914, -120.508004; area of occupancy 2.56 ha, 80 to 99 m elevation. This location was identified in 2015 by helicopter surveys for Lompoc yerba santa in potential habitat, with confirmation of 691 ramets by subsequent ground visitation. The Lompoc yerba santa are sparsely situated in gaps among dense Burton Mesa chaparral dominated by La Purisima manzanita with bishop pine and coast live oak.[7] ManTech[7] observed new growth of ramets in the understory of chaparral dieback in 2015 likely due to drought. Having surveyed this area by helicopter in 2022, M. Ball (ManTech, pers. comm. 2022) reported that most bishop pines had died during the prolonged drought and created openings in the chaparral.

2E Upper East Slope Pine Canyon (part of previous occurrence 3 in 1983 and 1994): Upper east slope of Pine Canyon; 34.704071, -120.509654; 100 m elevation, 58 m below the ridge crest. Smith (1983) identified this colony of 41 stems in diatomaceous shale. He marked the general location on a map, which we used to estimate latitude/longitude. The plants were in chaparral, with dominant species manzanita and occasional bishop pine. The vegetation cover was thin with large bare areas, which is where Lompoc yerba santa primarily occurred. Smith observed many stems connected by rhizomes and a lack of seeds in 1982, hypothesizing the colony is uniclonal. We visited the location in 2021 and saw no Lompoc yerba santa. Based upon similar details, we suspect that Smith may have erred in marking his map and the colony is actually part of 2D, which is 152 m to the south. Likewise, ManTech[7] surveyed the Pine Canyon area from helicopter in 2015 without detecting Lompoc yerba santa at Smith's marked location.

2F Pine Canyon Stand North Group (part of previous occurrence 3 in 1983 and 1994): Floor and lowermost east slope of Pine Canyon, 0.87 to 1.05 km northwest of junction with Santa Lucia Canyon; 34.702814, -120.510876; area of occupancy 0.43 ha, 45 to 61 m elevation. Howald (1987) reported a colony of large, healthy plants at the northern extent (34.703592, -120.511155; our determination from old map) of our polygon for this group in 1987. She observed eight individuals adjacent to a newly-graded dirt road (for heavy equipment to construct an oil pipeline nearby; Mooney 1986d), along with scattered coast live oak and coastal sage scrub species. A fence was subsequently erected to protect the colony. Myers (1987) reported some plants appeared to have benefited by the grading that occurred a few years earlier, growing from sprouts to 2.4 m tall. She speculated that crowding in the understory could subsequently suppress further sprouting and cause local decline. In the south half of our polygon for this group, Wilken (2011) observed 200 ramets on Monterey shale at 34.702411, -120.510625 (47 m elevation) with shrubs 2 to 3 m tall. Then Wilken (2012) and Knapp (2013c) reported 150 individuals here (stems <1 m not counted), with many large plants up to 3 m tall and many young ramets in open sites. They described the habitat as mixed oak woodland/coastal sage scrub with coast live oak, black sage and western poison oak *Toxicodendron diversilobum* on sandy soil. They identified no immediate threats but observed evidence of rooting by feral pigs and trail-bike activity (trail re-routed 2013) at edge of the colony, which Wilken (2012) believed to be the largest colony on Vandenberg Space Force Base. ManTech[9] identified purple pampas grass *Cortaderia jubata* at north end of Pine Canyon as a threat to Lompoc yerba santa downstream in 2010 (treated 2021), and also erosion. Three additional records for 2F are the following (our data).

34.703085, -120.511023; Pine Canyon Stand A, 50 m elevation; 11 ramets in high quality habitat of mixed oak woodland and sage scrub (Calif. sagebrush, coast live oak: Burton Mesa chaparral) on sandy shale in a deep layer of oak leaf litter in 2006. Most Lompoc yerba santa were rooted under oaks, with basal stems

[9] ManTech SRS Technologies. 2010. 2010 special status plants monitoring on Vandenberg Air Force Base, California. Lompoc, Calif., 13 pp.

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1.25 to 2.5 cm diameter, and arced into the sagebrush. In 2010, nine ramets were observed and with habitat rated high quality. ManTech[9] and USFWS (2011) referred to this group as Pine Canyon Stand A.

34.702656, -120.510761; Pine Canyon Stand B, 48 m elevation; 172 ramets in high quality habitat of mixed oak woodland and sage scrub (Calif. sagebrush, coast live oak, coyote brush: Burton Mesa chaparral) on sandy shale, some in a deep layer of oak leaf litter in 2006. The Lompoc yerba santa extended into the dirt road beyond protected fencing of barbed wire. Because some plants bore metal tags (like 2G), we conclude this location is part of Elam's (1994) study site for previous occurrence 3 (D. Elam, pers. comm. 2021). In 2010, 149 ramets were observed and with habitat rated high quality. ManTech[9] and USFWS (2011) referred to this group as Pine Canyon Stand B.

34.702060, -120.510575; Pine Canyon Stand C, 47 m elevation; 59 ramets in high quality habitat of mixed oak woodland and sage scrub (Burton Mesa chaparral) on sandy shale, with some in a deep layer of oak leaf litter in 2006. In 2010, 79 ramets were observed here and with habitat rated high quality. ManTech[9] and USFWS (2011) referred to this group as Pine Canyon Stand C.

2G Pine Canyon Stand South Group (Pine Canyon Stand D, part of previous occurrence 3 in 1983 and 1994: Pine Canyon, 0.75 km northwest of junction with Santa Lucia Canyon; 34.701528, -120.509944; area of occupancy 0.52 ha, 46 to 71 m elevation. The information is from ManTech[7] and our data. This location was identified as Pine Canyon Stand D in 2006 with 372 ramets (ManTech;[9] USFWS 2011) sparsely distributed in high quality habitat on soil described as sandy, shaley loam. It is the southmost location for Lompoc yerba santa in Pine Canyon. The plants are in the canyon bottom and also extend up the lower east slope, growing in the understory of oak woodland and ending at transition to mixed Burton Mesa chaparral and bishop pine forest that dominate the upper slope. Several plants upslope were growing through thick leaf litter, and many stems had diameters >7.6 cm. Because one plant bore a metal tag (like others at 2F), we conclude this location also is part of Elam's (1994) study site for former occurrence 3 (D. Elam, pers. comm. 2021). In 2010 and 2015, 423 ramets and 513 stems/428 ramets were observed in high quality habitat, respectively.

2H South Santa Lucia Canyon (Santa Lucia Canyon Stand #4): Upper half of west slope (including ridge crest) of Santa Lucia Canyon, 0.39 km north of junction with Pine Canyon; 34.698924, -120.506723; area of occupancy 1.35 ha, 43 to 98 m elevation. We collected tissue samples here in 2019. The location is sandy, loose slopes (tar sand) with chaparral (chamise), grass, coyote brush, La Purisima manzanita and coast live oak showing scars of having burned. ManTech[7] referred to this site as Santa Lucia Canyon Stand #4, which was so dense (estimated 6,000 ramets on 0.88 ha) in 2015 they could not access without damaging plants. The location is documented by herbarium specimen KE Hasenstab-Lehman 2133 in the Santa Barbara Botanic Garden.

Occurrence 9.—35th Street and Calif. Boulevard, Vandenberg Space Force Base (north base); 34.705430, -120.571230; extent of occurrence 1.2 ha, area of occupancy 0.77 ha, 116 to 119 m elevation. This occurrence is 137 m northwest of the junction of 35th Street and Calif. Boulevard. ManTech[5] reported two groups separated by a 35 m distance in 2019: 9A (our designation; 116 to 119 m elevation), an eastern group with 89 ramets on 0.11 ha; and 9B (114 to 116 m elevation), a western group with 227 ramets on 0.66 ha. The following numbers have been observed: 1987, <500 individuals; 1993, >100 ramets; 2006, 1,017 ramets; 2010, 807 ramets; 2015, 958 stems/733 ramets; 2016, 651 stems/616 ramets; 2017, 627 stems/507 ramets; 2018, 804 stems/617 ramets; and 2019, 743 stems (plus 83 dead stems)/316 ramets (Bittman and Berg 1987; Elam 1994; ManTech[5,7]; our data). The occurrence is 11 m north of 35th Street and 105 m west of Calif. Boulevard.[7] The plants are sparsely distributed on sandy, rocky loam in Burton Mesa chaparral (predominant species La Purisima manzanita, Santa Barbara ceanothus *Ceanothus impressus*, chamise), which was rated high quality in 2006, 2010, 2015 and 2019 (our data). Based upon the data, the occurrence is in decline, which KFS and ManTech[6] attributed in 2020 to prolonged periods of drought. In 2019, iceplant *Carpobrotus* spp., purple pampas grass, Monterey pine *Pinus radiata* and Tasmanian bluegum *Eucalyptus globulus* were threats in the habitat.[10] This occurrence is managed, and Vandenberg Space Force Base is targeting invasive plant species for removal in its vicinity. Using Google Earth aerial imagery (dated 9 July 2016), we observed the occurrence is in a flat and level landscape in an area likely desirable for future development, and 0.64 km northwest of occurrence 10. It was reported to be uniclonal with low genetic diversity (Elam 1994) and low seed production (Smith 1983; Elam 1994; Knapp 2013a; our data), and our data show low to moderate genetic diversity. In 1982, an experimental burn of one-half of this occurrence resulted in

[10] ManTech SRS Technologies. 2020. Lompoc yerba santa habitat restoration, 35th Street stand: year 6 - Vandenberg Air Force Base, California. Lompoc, Calif., 22 pp.

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vigorous sprouting from underground rhizomes of Lompoc yerba santa along with death of some stems and invasion by hottentot fig *Carpobrotus edulis* (Jacks et al. 1984). Fire had stimulated expansion by outward spreading of root systems with production of new stems (Jacks et al. 1984). Threats here include military activities, development, road maintenance, low seed production, invasive species, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

Occurrence 10.—35th Street and New Mexico Avenue, Vandenberg Space Force Base (north base); 34.702700, -120.564000 (best estimate based on Griffiths et al. 1987a, b); 126 m elevation, somewhere near this location. The coordinates are 70 m southwest of the junction of 35th Street and New Mexico Avenue, which is not a precise location but instead indicate the likely undeveloped parcel of land where the specimens were collected in 1987 (G. Walden, pers. comm. 2021). This occurrence is based solely on the two herbarium specimens collected by Griffiths et al. (1987a, b): CDA17708, and OBI69622. CDA105381 was previously considered a third specimen collected by Griffiths and colleagues at this occurrence, but it is actually a prior accession number for specimen CDA17708 (J. Alexander, pers. comm. 2021). Griffiths et al. (1987a, b) described the occurrence as "several open, laxly spreading shrubs with upright branches." Using Google Earth aerial imagery (dated 27 July 2016), we observed the stated coordinates are in a flat and level landscape at the north edge of an area of undeveloped land and immediately south of the general area intended for development at Vandenberg Space Force Base, and 0.64 km southeast of occurrence 9. The occurrence is likely extirpated. Searches in 2005, 2006, 2015, 2019 and 2021 did not find any Lompoc yerba santa. The stated coordinates are in a grove of invasive Monterey pine and *Eucalyptus* with invasive grasses on sandy soil, including perennial veldt grass *Ehrharta calycina* and ripgut brome *Bromus diandrus*. Vandenberg Space Force Base is targeting non-native, invasive plant species for removal in and near the area. In particular, Monterey pine are girdled to help conserve nearby chaparral. Threats here include military activities, development, small number of plants, invasive species, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

Occurrence 14 (new).—Airfield, Vandenberg Space Force Base (north base); 34.72951, -120.56286; extent of occurrence 1.0 ha, area of occupancy 0.26 ha, 111 to 114 m elevation. This occurrence is 240 m east of the south end of the airfield. It is a new occurrence we identified in 2019 during surveys for Lompoc yerba santa in potential habitat as part of a potential project. Our own mapping combined with ManTech[5] shows eight groups of plants in Burton Mesa chaparral (USAF 2019) with predominant species being La Purisima manzanita, coyote brush, chamise and black sage. The distribution of the eight groups suggests multiclonality for this occurrence. It is in a relatively flat landscape with sandy soil in dense chaparral, and with many plants along a trail. We and ManTech[5] observed 78 ramets/70 individuals in 2019. We collected tissue samples from 57 stems in 2019 for genetic analyses, with results showing low to moderate genetic diversity. A potential military project (MQ-9 Wing Beddown) threatened this occurrence along with removal of 1.8 ha of habitat (USAF 2020; USFWS 2020, 2021), however, the project will now occur in Florida. Although the proposed project would have included relocating Lompoc yerba santa to another location and outplanting individuals grown from collected seed (USFWS 2020), this would have been experimental because a previous attempt to relocate was not successful.[10] Threats here include military activities, development, small number of plants, dense vegetation, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures. Vandenberg Space Force Base is targeting non-native, invasive plant species for removal in and near the occurrence.

Occurrence 15 (new).—Upper Pine Canyon (North Pine Canyon), Vandenberg Space Force Base (north base); 34.707560, -120.512927; extent of occurrence 417 m^2, area of occupancy 51 m^2, 85 to 96 m elevation. Two colonies: 15A, 34.707731, -120.512940; 96 m elevation (2 stems/2 ramets on 1 m^2 in 2015); 15B, 34.707416, -120.512907; 85 m elevation (3 stems/2 ramets on 50 m^2 in 2015). The coordinates and information are from ManTech[7] and our data. This new occurrence was identified in 2015 by helicopter surveys for Lompoc yerba santa in potential habitat, with confirmation by subsequent ground visitation. It is the northmost location for the species in Pine Canyon, 1.54 km beyond its junction with Santa Lucia Canyon. The two colonies are separated by a 35 m distance in high quality habitat: Burton Mesa chaparral, with predominant species being coast live oak, chamise, sand mesa manzanita *Arctostaphylos rudis* and bishop pine. The soil is fine sand with white rocks, some under heavy leaf litter. This occurrence is across the steep incline of the northeast slope of upper Pine Canyon and 1/3 of the way up to the ridge crest. The genetic diversity is unknown because tissues have not been sampled. The occurrence appears to have not burned in the past 150 yr.[3] Threats here include military activities, small number of plants, dense vegetation, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

Occurrence 16 (new).—Lake Canyon, Vandenberg Space Force Base (north base); 34.713555, -120.507173; across gentle incline at top edge of southwest canyon wall overlooking lower Lake Canyon,

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1.1 km northwest of junction of Washington Avenue and Santa Lucia Canyon Road (near Lompoc Gate); 176 m^2 'area' (ManTech;[7] our data), 119 m elevation. This new occurrence was found in 2006 during landscape surveys for Lompoc yerba santa in potential habitat. There appears to be one colony of plants that we calculate to be over 181 m^2 using our data. The habitat is rocky sand in chaparral with La Purisima manzanita as predominant species, rated high quality in 2006, 2010 and 2015 (our data). Recorded numbers are the following: 2006, 20 ramets; 2010, 48 ramets; and 2015, 28 ramets.[7] We collected tissue samples for genetic analyses in 2019. This occurrence burned in the Azalea Fire in 1997.[3] Threats here include military activities, development, small number of plants, dense vegetation, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

La Salle Canyon Geographic Population

Occurrence 13 (new).—Upper La Salle Canyon, on ridge above tributary on north side, 74 m east of Santa Ynez Ridge Road, Vandenberg Space Force Base (south base); 34.627353, -120.549724; extent of occurrence 0.20 ha, area of occupancy 824 m^2, 220 to 233 m elevation. Two locations separated by a 53 m distance: 13A (north), 34.627561, -120.549869 at 233 m elevation; and 13B (south), 34.627211, -120.549481 at 220 m elevation. The occurrence was first observed in 2018 (our data) with 281 stems/258 ramets on sandy soil: 37 stems/36 ramets at the north location on 221 m^2, and 244 stems/222 ramets at the south location on 603 m^2. Our data show low genetic diversity. This occurrence is in maritime chaparral with dominant species being La Purisima manzanita, and other associated species including chamise and bishop pine. Part of the occurrence (13A all, 13B part) was burned by the Canyon Fire in 2016 (our data; SB Atlas Admin[3]). The habitat was rated high quality in 2018, with the tallest Lompoc yerba santa standing 1.3 m. Vandenberg Space Force Base is targeting non-native, invasive plant species for removal in and near the occurrence. Known threats here are military activities, low genetic diversity, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

Santa Ynez Mountains Geographic Population

Occurrence 5 (includes previous occurrences 0 [Elam 1994], 6, 7 and 8).—Hollister Ranch; 34.49438, -120.37509 center of occurrence, along Cresta Road and Cementerio Road on crest of west end of Santa Ynez Mountains (Tranquillon Ridge) and its slope immediately below, above the heads of four canyons (Bullito Canyon, Canyon del Cojo, Canyon del Gato, west fork of Barranca Honda have been mentioned) leading down to Pacific Ocean in southwest Santa Barbara County; extent of occurrence 0.85 km^2, <0.49 km^2 area of occupancy. The Santa Ynez Mountains and its crest are oriented in an east/west direction and likewise this occurrence of Lompoc yerba santa, extending from 34.493633, -120.362501 to 34.490091, -120.386147 for a straight-line distance of 2.21 km. Elevational records of the species here range from 274 m (at head of west fork of Barranca Honda; 1941) to 838 m (at the head of Canyon del Cojo; 1957), although these extremes appear erroneous because such elevations do not seem to exist in the mapped area (414 to 533 m) under consideration. Most of what is known about the occurrence is from Mooney (1986b, c) who mapped much of its distribution in 1986, reporting the species on Matilija sandstone. Mooney (1986b, c) saw many individuals on the main ridge (Cresta Road), mostly juveniles and a few adults, and fewer individuals on a side ridge (Cementario Road) at lower elevation. She reported the species to be scattered all along the higher ridge top, sometimes in cracks of rocks, and away from the road, near the road, in the road and in graded areas, and locally common on the lower ridge top. The occurrence spanned over several parcels of private property, including the intersections of parcels 43, 46 and 47, and also further west on parcel 22.[11] USFWS (2011) reported the species on six contiguous parcels. Other records (CDFW 2020) report the species growing as shrubs up to 2.4 m tall in disturbed, rocky, sandy soil on the sandstone ridge and slopes in disturbed areas of chaparral among chamise, La Purisima manzanita, buck brush *Ceanothus cuneatus*, black sage, *Baccharis* sp., and mugwort *Artemisia* sp. At Elam's (1994) three sampling sites for occurrence 5, she reported moderate seed production and found multiclonal genetic diversity to be high: sample size 49 stems, comprised of 20 clones with 0.87 diversity; sample size 26 stems, comprised of 17 clones with 0.97 diversity; and sample size 30 stems, comprised of 11 clones with 0.93 diversity. Our data show moderate to high genetic diversity for this occurrence. Hollister Ranch (5,666 ha) is privately owned with multiple landowners. There are 133

[11] Hollister-Ranch.com. 2021. Hollister Ranch listing map. Available from: http://www.hollister-ranch.com/maps.html. Accessed August 2021.

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parcels, each at least 40 ha, with options for residential development and agriculture subject to approval by County of Santa Barbara. Access to the ranch is gated, strictly controlled, and generally considered exclusive. The ranch is mostly undeveloped, with 2% of its area devoted to residential use (primary use), and the remainder a working cattle ranch (secondary use).[11] USFWS (2011) considered Lompoc yerba santa at risk by development of the six parcels on which the species was known to occur, and we have no additional information. We identify the following threats here in 2022: development, dense vegetation, lack of management, road vehicles running over plants, road maintenance, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

Occurrence 12.—Jack and Laura Dangermond Preserve; 34.5140944, -120.3725639; extent of occurrence 50 m^2, 355 m elevation, near boundary in eastmost part of preserve. The private property was previously a cattle ranch and it is mostly undeveloped. This occurrence with one colony was first observed in 2012 with a total of five individuals:[12] three small sprouts in the dirt road, and two mature individuals at a 3 m distance south of it. S. Batiuk (pers. comm. 2020) subsequently observed only the two mature individuals (with flowers) in May 2013 and May 2014, which he described as "robust and healthy" in a small, dense patch of coyote brush with buck brush on sandstone-derived soil. Batiuk (pers. comm. 2020) stated his work group searched for more Lompoc yerba santa in the area but found none; further, "we've been all over the ranch over the years we were on that project, and I would suspect that if there are more, it's going to be 1-few individuals at most." We visited the occurrence in 2022 and observed 12 stems (multiple heights up to 2.5 m, some with flowers) south of the dirt road (rarely used), all appearing vigorous and healthy, along with collecting tissues and a herbarium specimen (Guilliams 7655). The location is 60 m below the top (west side) of a north/south oriented foothill on the north side of the Santa Ynez Mountains, below Tranquillon Ridge (location of occurrence 5). The Jack and Laura Dangermond Preserve (99 km^2) is owned by The Nature Conservancy since 2017.[13] Threats here include small number of plants, presumed low genetic diversity, potentially uniclonalism, dense vegetation, lack of management, altered fire regime/fire management practices, and climate change with severe drought and increased temperatures.

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[12] WRA, Inc. 2017. Comprehensive biological resources report for the Cojo-Jalama Ranches, Santa Barbara County, California. San Rafael, Calif., 416 pp.

[13] Butterfield, H.S., M. Reynolds, M.G. Gleason, M. Merrifield, B.S. Cohen, W.N. Heady, D. Cameron, T. Rick, E. Inlander, M. Katkowski, L. Riege, J. Knapp, S. Gennet, G. Gorga, K. Lin, K. Easterday, B. Leahy and M. Bell. 2019. Jack and Laura Dangermond Preserve Integrated Resources Management Plan. The Nature Conservancy, Lompoc, Calif., 112 pp.